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NUMBERS 351-379

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CAMBRIDGE, MASS. 12 JUNE, 1970 NUMBER 351

A NEW SPECIES IN THE NOMEID FISH GENUS *PSENES* FROM THE EQUATORIAL EASTERN PACIFIC [1]

Richard L. Haedrich[2]

ABSTRACT. *Psenes sio* n. sp. is based on five specimens 23-66 mm SL from the equatorial eastern Pacific Ocean. The new species belongs to the species-group (others are *P. pellucidus, P. maculatus,* and *P. arafurensis*) with large, laterally compressed, knifelike teeth in the lower jaw. *P. cyanophrys* and *P. whiteleggii* have small conical teeth in both jaws. The new species is characterised by its light color, long pelvic fins, two weak anal spines and 23–24 rays, 18–19 pectoral finrays, and 36–38 vertebrae.

In a recent unpublished yet widely distributed manuscript (Haedrich and Horn, 1969), a new species of *Psenes* was included in a key (p. 36). It was stated explicitly that use of the name in the key did not constitute publication, and it was indicated that a formal description would soon appear in a review of the entire genus. Other responsibilities, however, have virtually brought this work to a halt, and early completion of the review does not seem likely. Therefore, in order to avoid the nomenclatural debacle that I see developing, this note has been prepared describing the new species.

The specimens upon which the new species is based were made available by Jørgen Nielsen, and are housed in Universitetets Zoologiske Museum, Copenhagen (ZMC). They were collected by Dr. Nielsen on Step-I, a cruise conducted by the Scripps Institution of Oceanography. The manuscript has been read by Richard H. Backus and Giles W. Mead. Figure 1 was drawn by E. Leenders.

[1] Contribution No. 2486 from the Woods Hole Oceanographic Institution.

[2] Woods Hole Oceanographic Institution, Woods Hole, Mass., and Museum of Comparative Zoology, Harvard.

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Among stromateoid fishes, the genus *Psenes* is distinguished in having two dorsal fins with the first dorsal originating over or before the pectoral insertion, persistent thoracic pelvic fins, a deep to moderately elongate body, and teeth present in some species on the palatines and/or basibranchials but never on the glossohyal. The genus, its relationships, and the nominal species were treated in a general way by Haedrich (1967), though recent findings will modify this account somewhat. Within *Psenes,* there seem to be two species groups. One group (including *P. cyanophrys* and *P. whiteleggii*) is characterized by small, conical, slightly recurved teeth in both the upper and lower jaw. The other group (including *P. pellucidus, P. arafurensis, P. maculatus* and the new species) has small, conical, slightly recurved teeth in the upper jaw and large, laterally flattened, bladelike teeth in the lower jaw.

In recognition of the considerable contributions to marine ichthyology made by the Scripps Institution of Oceanography, the new species will be known as

Psenes sio n. sp.
Figure 1

Material. Five specimens, 23-66 mm SL, all in ZMC; those marked with an asterisk* have been X-rayed: *1 spec., 60 mm SL, HOLOTYPE, Step-I sta. 23, 11°10′S 80°01′W, 17 Oct. 1960, 2250-2345 hrs., 0-90 m, 5′ net, surf. temp. 17.8°C. PARATYPES: *1 spec., 66 mm SL, Step-I sta. 80-1, 1°24′S 94°55′W, 2/3 Dec. 1960, 2335-0230 hrs., high-speed net, battered. 2 spec., 26 & 44 mm SL, Step-I sta. 73-1, 4°22′S 95°04′W, 2 Dec. 1960, 0200-0500 hrs., high-speed net, very battered, smaller spec. cleaned-and-stained. *1 spec., 23 mm SL, Step-I sta. 80, 1°59′S 94°55′W, 2 Dec. 1960, 2200 hrs., dipnet-nightlight, surf. temp. 22°C. All specimens are immature.

Diagnosis. An elongate, compressed, light-colored *Psenes* with large, compressed close-set teeth in the lower jaw, long pelvic fins, two weak anal spines and 23-24 rays, and 36 to 38 vertebrae.

Description. Individual proportions and counts are presented in Table 1.

The body is elongate, the maximum depth of larger specimens

being around 30 per cent of the standard length, and is very compressed. The caudal peduncle is tapered, compressed, and somewhat elongate. The musculature, though firm, is translucent, particularly along the anal fin base and over the viscera. The two dorsal fins are scarcely divided. The first dorsal fin originates over the edge of the opercle and comprises 10 to 12 thin brittle spines, the second originates just behind mid-body and comprises 23 to 25 long rays. The entire fin folds partially into a very shallow groove and terminates behind the end of the anal fin. The anus is at mid-body, in a slit. The anal fin commences shortly behind the anus under the third or fourth ray of the second dorsal, and is composed of two weak spines and 23 or 24 long rays. The muscles for elevating the anal rays can be clearly seen, as can the basal elements of both median fins. The pectoral fin is long and fairly broad, with 18 or 19 rays; its base is inclined about 45° to the vertical. The pelvic fins are very long; they insert under the middle or end of the pectoral fin base and extend beyond the anal origin, and are composed of one short spine and five long branched rays. The caudal fin, broken in most specimens, is apparently long and forked; the small elements preceding the principal rays extend well forward on the peduncle. The cycloid scales are very small, and do not appear to extend significantly onto the bases of the median fins. The scales are extremely deciduous, and most are gone; the count of scale pockets along the lateral line of the holotype is ca. 85. The skin is thin; the subdermal mucus canal system is but little developed, and the body pores are very small or wanting.

The head is around 35 per cent of the standard length, its profile sloping. The skin of the top of the head is naked, and pores are clearly visible, particularly those over the head of the hyomandibular. The eye is of moderate size, located a little more than its diameter from the tip of the truncate snout, and does not enter into the profile of the head. There is apparently no adipose tissue around the eye, but somes does extend forward from the front of the eye to surround the nostrils. The two small nostrils are located much nearer to the tip of the snout than to the eye. The end of the maxillary is below the anterior border of the eye, but the angle of the gape is well before the eye. The premaxillary is not protractile. The lacrimal bone is large and transparent, and covers the top of the maxillary. The teeth are uniserial in the jaws. The teeth in the upper jaw are small, conical, slightly recurved, and spaced; the teeth in the lower jaw are large, at least twice as long

as those in the upper jaw, compressed and knifelike with very small cusps, and very close-set. The vomer, palatines, and basibranchials appear to be toothless. The oral valves are prominent. The opercles are very thin; their margins are either entire or set with extremely fine spinules. The striated opercle has two very weak flat spines; the angle of the preopercle is rounded but does not bulge backward. The gill-rakers are moderate, blunt, about half the length of the filaments, and bear fine teeth on their inner edges; the rakers are spaced, about 15 on the lower limb of the first arch. The pseudobranch is well developed, but there are no rudimentary rakers below it. The light yellow thymus is clearly visible. There are six branchiostegal rays.

The color in alcohol is tan, darker on the back than on the sides. There is a suggestion of three brownish vertical bands on the after part of the body in some specimens. The first dorsal fin is dark, but all the other fins are whitish. The dark lining of the gill cavity shows clearly through the transparent opercles. The dark peritoneum shows clearly through the thin abdominal wall. The inside of the mouth is light yellow, and the eye is grey.

The skeleton in general is very light. This is particularly apparent in the thin transparent dermal skeleton. There is no supramaxillary bone. The supraoccipital is but little developed. There is a wide opening between the cleithrum and the coracoid. The pelvic bones reach to the cleithrum. There is a large foramen in the scapula. The postcleithrum can be plainly seen through the body wall, and it extends to the lower margin of the body. There are 36 to 38 vertebrae, including the hypural; about 12 to 15 vertebrae appear to be precaudal. In the tail, there are two autogenous haemal spines, four hypurals, two paired uroneurals, and three epurals. The second and third hypurals are broad triangular plates much larger than any other caudal element. The first hypural bears an hypuropophysis. Three free interneurals precede the dorsal fin. The first dorsal interneural supports two spines. The two anal spines are weak.

Remarks. Most species of *Psenes* are widely distributed in the tropical and sub-tropical parts of the world ocean. *P. sio,* however, is quite restricted, and has been found only in the eastern Pacific from about 11° S (holotype) to perhaps 10° N (R. Rosenblatt, additional Scripps specimens, *in litt.*). *P. sio* most closely resembles *P. maculatus,* an apparently antitropical species known only from sub-tropical waters in the North and South Atlantic.

Within the range of *Psenes sio,* only *P. cyanophrys* is known to occur for sure. This species may be distinguished from *P. sio*

by its small conical teeth that are similar in both jaws (as mentioned above), its color pattern of fine horizontal stripes (*P. sio* has about three indistinct vertical bands), its greater maximum depth (43-52% SL *vs.* 29-41% SL in *P. sio*), its generally greater number of median fin rays (D 24-29 *vs.* 23-25, A 24-28 *vs.* 23-24), and its fewer vertebrae (31 *vs.* 36-38).

As yet unrecorded from the eastern tropical Pacific but known from the western parts of that ocean are *Psenes pellucidus* and *P. arafurensis.* The former has more median finrays and vertebrae (D 27-32, A 26-31, vert. 41-42) than *P. sio,* the latter fewer (D 18-22, A 20-22, vert. 31).

Psenes whiteleggii, from the Indian Ocean and Australia, has conical teeth in both jaws and low median finray and vertebral counts (D 17-20, A 17-18, vert. 31-32). The Atlantic *P. maculatus,* the species most similar to *P. sio,* has slightly fewer median finrays and vertebrae (D 22-24, A 22-24, vert. 35) and more pectoral finrays (21-22 *vs.* 19 in *P. sio*) and anal spines (III *vs.* II). The preanal distance is 58-63% SL in *P. maculatus,* and 51-54% SL in *P. sio.*

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(Received 2 April 1970.)

TABLE 1

Measurements and counts of *Psenes sio* n. sp.

	HOLOTYPE Step-I, sta. 23	PARATYPES: Step-I, sta. 80-1	Step-I, sta. 77-1		Step-I, sta. 80
Total length	74.5 mm	> 75 mm	— mm	— mm	26.5 mm
Standard length	60.3	65.8	43.7	25.7	23.4
Head length	21.7	22.1	13.5	—	8.4
Snout	5.7	5.6	—	—	2.1
Eye diameter	6.5	6.2	—	—	3.1
Length upper jaw	5.8	6.2	—	—	3.0
Interorbital width	5.5	—	—	—	2.8
Pectoral length	15.2	15.5	11.0	6.9	5.9
Pelvic length	13.4	—	11.4	6.8	6.1
Longest D_1 spine	—	—	—	—	3.5
Predorsal distance	21.9	22.4	15.6	9.8	9.3
Preanal distance	31.5	34.1	21.4	13.2	12.6
Maximum depth	18.5	19.5	13.5	10.3	9.6
Depth peduncle	4.3	4.4	3.2	1.8	2.2
Counts:					
D	X, 23	XII, 25	XII, 25	XII, 25	XII, 24
A	II, 24	II, 23	II, 23	II, 23	II, 23
P	19	19	18	19	—
Gill rakers	7+1+14	8+1+15	8+1+17	—	—
Lat. line scales	85 ?	—	—	—	—
Vertebrae	15+23	15+23	—	15+23	12+24

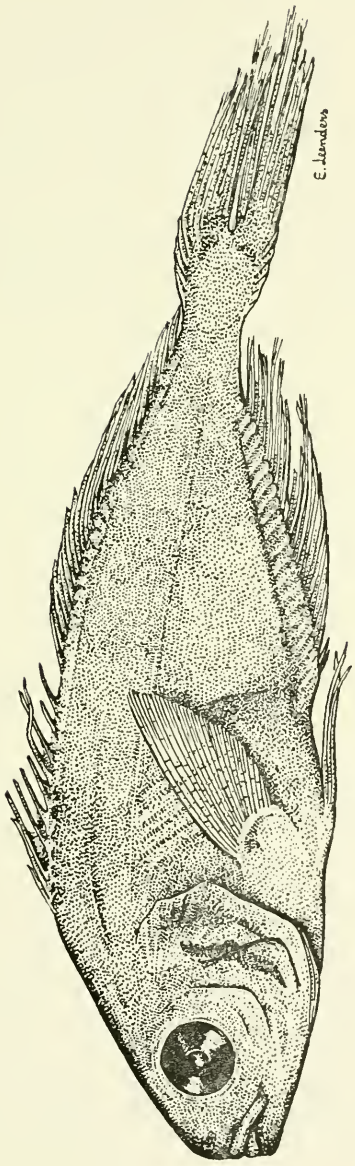

Figure 1. Holotype of *Psenes sio* n. sp., 60 mm SL, 11°10'S, 80°01'W. ZMC specimen, drawn by E. Leenders.

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CAMBRIDGE, MASS. 10 JULY, 1970 NUMBER 352

THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA VII. THE POSTCRANIAL SKELETON OF THE TRAVERSODONTID *MASSETOGNATHUS PASCUALI* (THERAPSIDA, CYNODONTIA)

Farish A. Jenkins, Jr.[1]

ABSTRACT. The postcranial skeleton of *Massetognathus pascuali* is described from a single nearly complete individual and four disarticulated specimens; manus, pes and pubis could not be described from the available material. *M. pascuali* has a postcranial skeleton morphologically similar to that in *Pascualgnathus polanskii* (an earlier traversodontid) and in African Triassic cynodonts. The basic skeletal pattern of all these forms differs from that in *Exaeretodon* sp., an advanced traversodontid. The specialized, imbricating ribs of *M. pascuali* are intermediate in form between those of *P. polanskii* (which are diademodontid in form) and those of *Exaeretodon* sp. (which essentially have lost the cynodont specialization).

Although Richard Owen made the first study of a cynodont more than a century ago, a detailed knowledge of cynodonts has accumulated only recently. First known only from Africa, representatives of this advanced group of mammallike reptiles have now been recovered from Asia and North and South America. The most specialized and, during the early and middle Triassic, the most abundant cynodonts were the herbivorous gomphodonts. Transversely broad, multicuspid postcanine molars with heavy occlusal wear (often to the point of effacing the original crown pattern) are characteristic of the group. Romer (1967) recognized three gomphodont families: Diademodontidae, Traversodontidae, and Trirhachodontidae. *Massetognathus pascuali* is a traversodontid and is one of two species described by Romer (1967) from the

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Chañares Formation of Argentina. Other undoubted traversodontid genera include *Traversodon* from the Santa María Formation of Brasil, *Exaeretodon, Proexaeretodon* and *Ischignathus* from the Ischigualasto Formation of Argentina, and *Scalenodon* and *Scalenodontoides* from the Manda and Molteno beds, respectively, of Africa. *Pascualgnathus polanskii* from the Puesto Viejo Formation of Argentina, originally classified as a diademodontid (Bonaparte, 1966a; 1966b), is now interpreted as a primitive traversodontid on the basis of tooth morphology (Bonaparte, 1967, and personal communication).

The present account of the *Massetognathus pascuali* postcranial skeleton is based upon the disarticulated remains of at least four individuals and an almost completely articulated skeleton of a fifth individual, all about the same size and preserved in a nodule several inches thick and two and one-half feet in diameter. The 1964-65 expedition of the Museo de la Plata and Museum of Comparative Zoology collected the nodule from the Chañares Formation in the Chañares-Gualo region of western Argentina. All the skeletal material is catalogued as No. 3691 in the Museum of Comparative Zoology.

Although the available postcranial material of *Massetognathus pascuali* is incomplete, there are two reasons why even a partial account is important. First, some workers regard cynodonts as ancestral to mammals (Crompton and Jenkins, 1968; Hopson and Crompton, 1969). Gomphodont cynodonts are certainly not directly related to mammals, but they undoubtedly possessed a degree of biological organization that at least approximated that of their carnivorous-insectivorous relatives (from some form of which mammals were derived). Thus all cynodonts are relevant to evaluating the reptile-mammal transition. Second, most published investigations of cynodonts have been restricted to cranial anatomy. Well-preserved, generically determinate postcranial skeletons are rare. Of South American genera, only *Belesodon* (von Huene, 1935–1942), *Exaeretodon* (Bonaparte, 1963a) and *Pascualgnathus* are known from relatively complete skeletons; the preservation of known *Belesodon* material is poor, however, and *Exaeretodon* appears to be morphologically aberrant in comparison to the general pattern known from other cynodonts. Postcranial material associated with *Traversodon* and *Chiniquodon* (von Huene, 1935–1942) is only fragmentary, although Romer (1969) has recently described more complete limb bones of *Chiniquodon*. I have reviewed the postcranial skeletons of African cynodonts (Jenkins, in

press). Of the Russian forms very little is known; some data is available for *Permocynodon* (Konjukova, 1946).

Vertebral column and ribs

The number of presacral vertebrae in *Massetognathus pascuali* is at least 23 and is here interpreted to be about 26. A hiatus in the lumbar series of the one nearly complete, articulated vertebral column is responsible for this uncertainty. Present are 7 cervicals, 16+? dorsals, and 6 sacrals. Judging from the length of several articulated but incomplete caudal series, tail vertebrae numbered at least 17 and probably as many as 25. A count of 26 presacral vertebrae in *M. pascuali* compares with 26 in *Leavachia duvenhagei* (Broom, 1948), 27 in *Thrinaxodon liorhinus* (Jenkins, in press), 28 in *Exaeretodon* sp. (Bonaparte, 1963a), 29 in *Cynognathus crateronotus* (Seeley, 1895) and at least 30 in a large cynodont identified tentatively as *Diademodon* sp. (Brink, 1955; Jenkins, in press).

Two separately articulating atlas arches appear to conform to the general pattern known from African Triassic cynodonts (Jenkins, in press), but their preservation is too poor to allow specific description or comparison. The atlas intercentrum, transversely elongate and ventrally convex, bears a posteriorly directed process or lip (l, Fig. 1B). A concave articular facet on the dorsal surface of this lip contacts a median convex facet on the anterior aspect of the atlas centrum (f a i, Fig. 6B). The lateral extremities of the intercentrum each bear, on their dorsal surfaces, a concave facet that articulates with the ventral aspect of one of the two occipital condyles. The atlas centrum (6 mm long) is synostosed

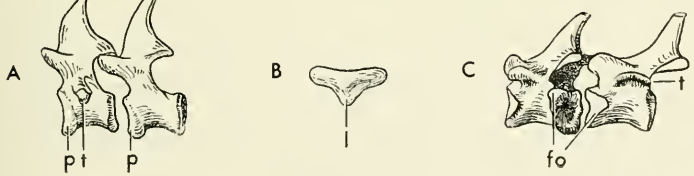

Figure 1. Vertebral elements in *Massetognathus pascuali*. *A*, Cervical vertebrae, probably the third and fourth, in lateral view. *B*, First or atlantal intercentrum in ventral view with anterior margin toward the top of the page. *C*, Anterior dorsal ("thoracic") vertebrae; vertebra on the right is in lateral view, on the left posterolateral view. All × 1. Abbreviations: fo, costal fovea for rib head; l, posterior lip of the intercentrum; p, parapophysis; t, transverse process.

to the axis centrum (8.5 mm long), forming a conspicuously large vertebra. On the dorso-lateral aspects of the atlas centrum are two facets, one for each atlas arch half (f a a, Fig. 6B). Protruding from the median aspect of the centrum between these facets is a small process (d, Fig. 6B) homologous with the dens or odontoid process of mammals. Elsewhere (Jenkins, 1969; in press) I have proposed that the mammalian dens originated as a neomorphic process from the atlas centrum of cynodonts. The occurrence of a dens in *Massetognathus pascuali* is unequivocal and supports the theory that both a dens and an atlas centrum (of which the dens was formerly thought to be a vestige) occur together among cynodonts.

The axis centrum of the one articulated cervical series is about 9 mm long, 1 mm longer than the centra of the following cervicals. The axial prezygapophyses have been broken off on all specimens, but from the appearance of their narrow bases—no thicker than the laminae from which they protrude—they are vestigial. Axial postzygapophyses of normal size bear articular facets at an angle estimated to be 25° to the horizontal. The axial spine, a flat blade with a distinctly mammalian shape, exhibits a straight dorsal margin that was probably slightly convex during life. The robust transverse processes are directed posterolaterally.

Cervical centra are amphicoelous, as are all other centra in *Massetognathus pascuali,* with the exception of the atlas (only the posterior aspect bears a notochordal concavity) and possibly some of the smaller caudal vertebrae. In cervical vertebrae, the rim surrounding the notochordal concavity on each end is swollen, and this increases the concave curvature of the sides and ventral aspect of each centrum. A bulbous parapophysis is to be found on the ventrolateral aspect of each anterior rim (p, Fig. 1A). If the rib head articulated on the apex of the parapophysis, as seems most likely on the basis of the large size of the process, then this condition differs from that in species of *Thrinaxodon* and *Cynognathus,* in which cervical rib heads are situated intervertebrally. A median ventral keel, similar to that in other cynodont cervicals, traverses the length of each cervical centrum.

Cervical pedicles are narrow anteroposteriorly and bear short, stout transverse processes (t, Fig. 1A). Cervical spines, broken off on all but two disarticulated cervicals (Fig. 1A), are transversely slender and recurved, and taper abruptly toward the apex. Of particular interest are the zygapophyses, which provide a basis for distinction between cervical and dorsal (anterior thoracic) vertebrae. As noted above, the axial postzygapophyseal facets are

oriented at an angle of about 25° to the horizontal; the orientation of posterior facets on the third through sixth cervical are more than 25°—probably about 35°. The distance between their lateral margins is approximately 7 mm. The anterior articular facets of the seventh cervical of course conform in orientation and spacing to those of the foregoing series. The posterior articular facets, however, appear to be oriented at about 45°. Those on the succeeding (eighth) vertebra are nearly parasagittal—i.e., within a few degrees of vertical—and are only 3.5 mm apart. The articular facet characteristics of the eighth vertebra, continued (with gradual modification) through the dorsal series, definitely establish a different pattern. Although transitional, the seventh vertebra most closely resembles other neck vertebrae and thus may be regarded as the last cervical. Similar changes in facet orientation and spacing, together with other morphological changes, occur between the seventh and eighth vertebrae of *Thrinaxodon liorhinus* and *Cynognathus crateronotus* (Jenkins, in press). The condition in *Massetognathus pascuali* reaffirms the fact that the "mammalian" number of seven cervical vertebrae was already established in cynodonts.

With the exception of the atlas intercentrum, no other cervical intercentra have been identified. The broad grooves formed by the rims of adjacent centra are evidence that intercentra were present—as in *Thrinaxodon liorhinus,* for example—and the state of disarticulation accounts for their postmortem loss.

The dorsal vertebral column in cynodonts is either a relatively undifferentiated dorsal series (as in most reptiles) or two series—"thoracic" and "lumbar" (as in mammals). In certain African Triassic cynodonts, separation of thoracic and lumbar regions may be made on the basis of distinct morphological specializations of the posterior dorsal (= lumbar) ribs (Jenkins, in press). In other cynodonts (e.g., *Exaeretodon* sp.; Bonaparte, 1963a) the trunk cannot be divided into thoracic and lumbar regions because the posterior ribs are not specialized. *Massetognathus pascuali* has specialized "lumbar" ribs and clearly belongs to the first category. The exact number of thoracic and lumbar vertebrae is unknown because a complete vertebral column with ribs is not yet available. Therefore, thoracic and lumbar vertebrae will be given only a general description as anterior and posterior dorsals, respectively, although the ribs (to be discussed below) clearly give evidence of a differentiated series.

The centra of anterior dorsal vertebrae are approximately 8.5 mm long; those of posterior dorsals are about 11 mm long (10 mm

in the one articulated specimen). The costal foveae (fo, Fig. 1C) of anterior dorsal vertebrae form a cleft for reception of the rib head, which is therefore intervertebral in position. On posterior dorsals the rib head articulates with a parapophysis (p, Fig. 2B) and is not intervertebral. Transverse processes are laminar and bowed dorsally on anterior dorsal vertebrae (t, Fig. 1C) but are rodlike and round in cross-section on posterior dorsals (t, Fig. 2B). The posterior intervertebral notch is deep throughout the dorsal series, the anterior notch negligible or absent. In contrast to many cynodonts, anapophyses are lacking. Dorsal prezygapophyses are robust, extending to or slightly beyond the level of the anterior aspect of the centrum. Articular facets on the first dorsal vertebra are about 3.5 mm apart and on the ninth are 4.0 mm; an abrupt widening takes place at some point in the middle or posterior dorsal series, for the articular facets of the penultimate dorsal vertebra are about 7 mm apart. The narrowly-spaced facets of anterior dorsals are nearly vertical, whereas those wider apart on the posterior dorsals are oriented at angles of as much as 45°. Neural spines on anterior dorsals are narrow, but unlike cervical spines, do not taper significantly at the apex; they incline caudad at angles of about 30°. Spines on posterior dorsal vertebrae are broad anteroposteriorly, leaving only a narrow gap between vertebrae; their inclination is only a few degrees caudad.

Sacral vertebrae successively decrease in size posteriorly. The centrum of the first sacral is approximately as long as those of the posterior dorsals (about 10 mm), while the sixth and last sacral centrum is some 2 mm shorter. Massive synapophyses—representing fused parapophyses and transverse processes—arise from the pedicles and from the anterior half of the side of the centrum. The zygapophyses, proportionately less robust than in the dorsal series, diminish in size on successively more posterior sacrals. In contrast to the orientation and spacing in the posterior dorsals, sacral articular facets incline nearly parasagittally and are narrowly spaced. At the last dorsal-first sacral articulation, the facets are 5.5 mm apart, but between the third and fourth and fourth and fifth sacrals they are only about 2 mm apart. At the fifth-sixth sacral articulation the trend is reversed; the facets are spaced 3.5 mm apart and appear to be inclined at 10° from the vertical. The trend toward less verticality of facets is continued into the caudal series. Sacral spines successively diminish in height and anteroposterior breadth. The spine on the first sacral is approximately 8 mm in height and 7 mm in breadth (*versus* 8.5 mm height and 8 mm breadth for the last dorsal spine). On the fifth sacral

the same measurements are 5.5 mm and 4.2 mm respectively. This trend is continued into the caudal series. The apices of sacral spines tend to be oval in contrast to those of the posterior dorsals which are elongate and attentuated at each end.

Caudal centra decrease in length from 6.5 mm at the first caudal to about 5 mm at the fifth. More posterior caudals preserved with MCZ 3691 are disarticulated, and their position cannot be positively assigned. However, one isolated series of eleven caudals shows a decrease in centrum length from 5 mm (which is evidence that it is approximately the fifth caudal) at the first to 4 mm at the last (? fifteenth caudal). Other specimens show that at least the first five caudals bear synapophyses. Articular facets are inclined at approximately 45°, at least through the first five caudals. The width between the lateral edges of these facets decreases from 6 mm (between the last sacral and first caudal) to 4.5 mm (between the fourth and fifth caudals). The terminal caudal is unknown.

Massetognathus pascuali probably possessed ribs on all presacral vertebrae, as in other cynodonts for which adequate material is known. Ribs were not found in association with the first six cervical vertebrae, although the morphology of the transverse processes and parapophyses on the axis through sixth cervical is clear evidence of their existence. These features cannot be verified at present on the atlas. The ribs of the seventh cervical appear to have been shorter than, but otherwise similar to, those of the anterior dorsal series.

Dorsal ribs in *Massetognathus pascuali* are of basically two types: in the anterior and middle dorsal series, a freely articulating rib of normal costal form and proportions, and in the posterior dorsal series, a fused rib with a Y-shaped distal end. Unfortunately, the transitional ribs between the two types are as yet unknown.

The proximal ends of anterior and middle dorsal ribs are basically triangular. The tuberculum and capitulum form two corners of the triangle; the shaft arises from the third (Fig. 3A). On the anterior aspect of this triangular surface is a slight crest (c, Fig. 3A) comparable to a similar feature on the anterior dorsal ribs of *Cynognathus* sp. (c, Fig. 3B, C). There is no other apparent feature that makes this type of rib distinctive. The maximum widths of the shafts near their proximal ends are between 2.5 and 3 mm. The distal ends, as preserved, are approximately 1.5 mm thick. Ribs of this basic morphology (as opposed to the specialized posterior

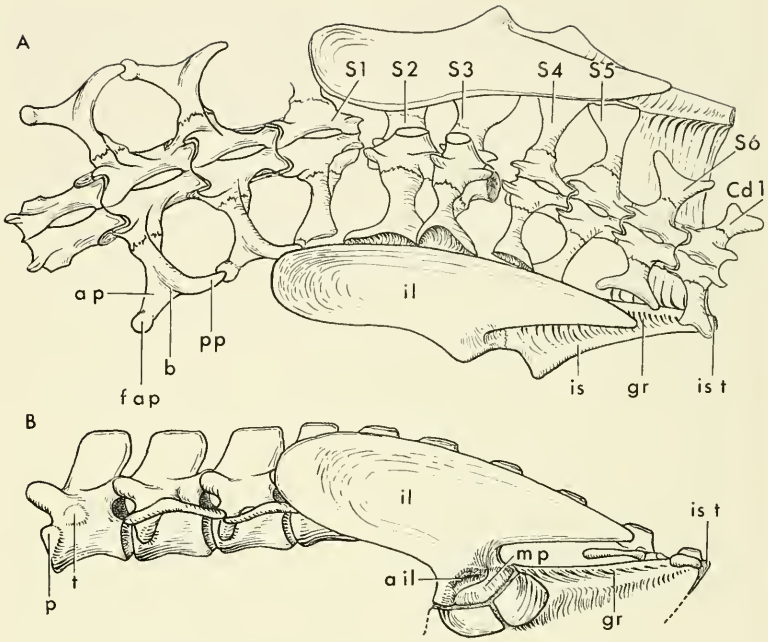

Figure 2. The posterior dorsal and sacral region in *Massetognathus pascuali* in *A*, dorsal and *B*, lateral views. × 1. Abbreviations: a il, acetabular facet of the ilium; a p, anterior process of rib shaft; b, ridge on dorsal aspect of rib shaft; f a p, articular facet on anterior process of rib shaft; gr, groove on dorsal margin of ischium; il, ilium; is, ischium; is t, ischial tuberosity; m p, medial process on base of ilium for articulation with ischium and pubis; p, parapophysis; p p, posterior process of rib shaft; t, transverse process.

dorsal ribs to be described next) are associated with at least the first thirteen dorsal vertebrae.

The following description of the specialized posterior dorsal ribs is based on the penultimate and last dorsal ribs preserved in articulation (Fig. 2) and in addition, a few disarticulated pieces of similar morphology. These ribs have a short shaft that bifurcates into a Y-shaped terminus with two processes (ap, pp, Figs. 2, 4B). The anterior process is broader than the posterior and bears, on the dorsal surface of its tip, a rather flat, round facet (f a p, Figs. 2A, 4B). Articulating with this facet is the end of the posterior process of the preceding rib. Presumably, the underside of the

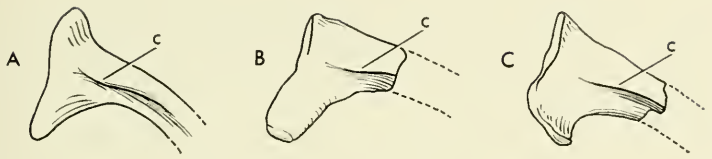

Figure 3. Proximal ends of dorsal ribs of *A, Massetognathus pascuali* (× 2), and of *B* and *C, Cynognathus* sp. (× ½) in anterior view. Abbreviations: c, crest on anterior aspect of shaft (see text for details).

posterior process also bears a facet. The rib as a whole projects laterad from the vertebral column and appears not to have had any ventral curvature. In lateral view (Fig. 2B) the shaft and point of bifurcation are at approximately the same level, but the anterior and posterior processes incline somewhat ventrally. A low, bony ridge (b, Figs. 2A, 4B) runs obliquely onto the posterior process from the point of bifurcation where it is most prominent. This feature is comparable to a similar ridge on the ribs of *Cynognathus* sp. (b, Fig. 4A) and other cynodonts; in the fourteenth thoracic

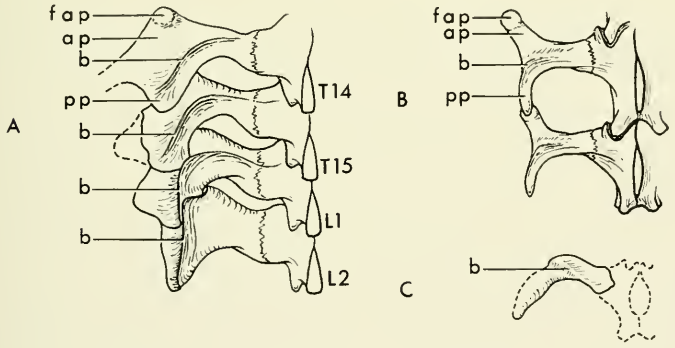

Figure 4. Specialized posterior dorsal ("lumbar") ribs of various cynodonts. *A, Cynognathus crateronotus* (British Museum of Natural History no. R. 2571), × ¼. *B, Massetognathus pascuali*, × 1. *C, Leavachia duvenhagei* (Rubidge Collection, Graaf Reinet, South Africa, no. 92), × ½. All dorsal views. Abbreviations: a p, anterior process of rib; b, ridge on dorsal aspect of rib shaft (of unknown function but probably homologous in the forms shown here); f a p, articular facet on anterior process of rib shaft; L1, L2, first and second lumbar vertebrae; p p, posterior process of rib shaft; T14, T15, fourteenth and fifteenth thoracic vertebrae.

rib of *C* (T14, Fig. 4A), the ridge is merely a linear elevation on the flat costal plate. On successive ribs, however, the ridge becomes more prominent until, in the lumbar ribs (L1, L2, Fig. 4A), it reflects forward to contact the preceding rib plate (see Jenkins, in press). No such reflection is evident in *Massetognathus pascuali,* but the ridge morphology and general pattern of the process are nevertheless similar to that of the fourteenth and fifteenth thoracic rib plates of *C.*

Specialized, imbricating ribs are common but not universal among cynodonts. Known members of the earliest cynodont family, the procynosuchids, apparently did not possess this specialization (see discussion below, however, for a possible exception). Galesaurids, typified by the well known *Thrinaxodon liorhinus* (Jenkins, in press), developed costal expansions on all presacral ribs. Members of three other families, e.g., *Cynognathus crateronotus* (Cynognathidae; Seeley, 1895), *Diademodon* sp. (Diademodontidae; Jenkins, in press) and *Cricodon metabolus* (Trirachodontidae; Crompton, 1955), possessed imbricating ribs only in the posterior dorsal region. The ribs in chiniquodontids (von Huene, 1935-1942) are as yet unknown. There remains only the Traversodontidae, which Bonaparte (1963b) characterized, on the basis of species of *Exaeretodon* and supposedly *Traversodon,* as lacking synostosed ribs with overlapping processes. For this and other reasons, Bonaparte interpreted traversodontids as probably having arisen from procynosuchids along a lineage separate from that ancestral to all other cynodont families (whose members possess rib specializations). However, *Massetognathus pascuali* unquestionably possesses synostosed lumbar ribs with details comparable to the *Cynognathus-Diademodon* pattern. *Pascualgnathus polanskii,* now classified as a traversodontid (Bonaparte, 1967), has lumbar ribs that are unquestionably diademodontid in pattern. Furthermore, von Huene (1935–1942; 137-140) described expanded ribs ("Fächerrippen") synostosed to the lumbar vertebrae in *Traversodon stahleckeri.* Crompton (1955) presented circumstantial evidence that the traversodont *Scalenodon* from the African Manda beds also possessed the expanded rib specialization. Yet Bonaparte (1963a) amply demonstrated that at least one traversodont, *Exaeretodon* sp., did not possess such specialization. Presacral ribs in *Exaeretodon* sp. are morphologically uniform and are more or less freely articulating (although the more "solid" attachment of the last three dorsal ribs, as described by Bonaparte, possibly represents a vestige of a less mobile articulation typical of expanded ribs). In view of this unexpected association at the family level of

forms possessing and forms lacking rib specializations, the taxonomic significance of this character should be reassessed. Further comment is reserved for the discussion below.

Sacral ribs in *Massetognathus pascuali* have an essentially confluent capitulum and tuberculum, a short shaft and an expanded distal end for articulation with the iliac blade. Proximally each rib is synostosed to its corresponding vertebra. If I may judge from the disarticulated condition of every known sacroiliac joint, ligaments and cartilage must have been chiefly responsible for binding the ilium and sacral ribs. The concave distal ends of the sacral ribs conform to the gently convex internal surface of the ilium, but they do not appear to form any osseous interdigitation by which sacroiliac joints are commonly reinforced. Viewed from above, the distal end of the first sacral rib (S1, left side, Fig. 2A) is Y-shaped with processes directed anterolaterad and posterolaterad. Articulating with the dorsal surface of the anterolateral process is the posterior process of the last dorsal (lumbar) rib. The second sacral rib has the largest distal expansion; irregularly shaped and widest anteriorly, the expansion is 7 mm long in one well preserved specimen. The third, fourth and fifth ribs bear more or less symmetrical distal expansions that are successively smaller caudally. The first four sacral rib shafts are oriented more or less laterally, the fifth slightly anterolaterally. The sixth and last sacral rib bears a shaft that is directed posterolaterally and a bifurcated, Y-shaped terminus resembling that of posterior dorsal ribs. Its iliac articular surface is narrow and strap shaped; the rib and vertebra could well be interpreted as the first caudal were it not for its position opposite the posterior tip of the iliac blade (S6, Fig. 2A). While it is apparent that the width between the distal ends of this pair of ribs (20 mm) is much less than that of the fourth and fifth sacrals (27 mm), the intervening gap could well have been completed by ligaments. This interpretation of the sixth sacral vertebra and ribs may be open to future modification, but on present evidence appears to be the most probable.

Only the first three caudal ribs are preserved. All are synostosed, their shafts directly posterolaterally. The first is only 8 mm long (Cd1, Fig. 2A), with two blunt processes on its terminus resembling a stunted version of the last sacral rib. As far as can be determined, terminal processes were not developed on the second and third caudal ribs, which are 5 mm or less in length. Ribs on succeeding vertebrae must have been very small and probably did not occur in the posterior caudal series.

Shoulder Girdle

Available interclavicles of *Massetognathus pascuali* are incomplete, although there is sufficient material to conclude that the morphology is very similar to that in *Thrinaxodon liorhinus* and different from that in *Exaeretodon* sp. In outline the interclavicle is cruciate with an elongate posterior ramus (pr, Fig. 5A). The entire bone, although basically a flat plate, is bowed ventrally from front to back. Two ridges, one longitudinal, the other transverse, divide the ventral surface of the interclavicle into quadrants. The two anterior quadrants (c c, Fig. 5A) are shallow concavities for reception of the proximal ends of the clavicles. The ridges are

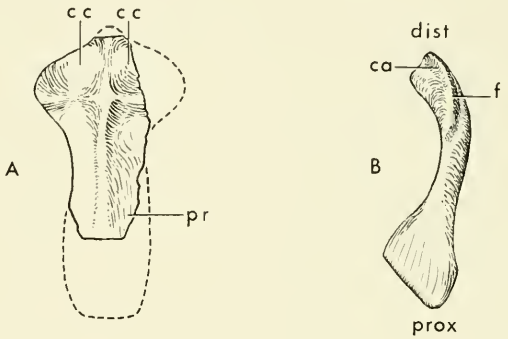

Figure 5. *A*, The interclavicle and *B*, the right clavicle of *Massetognathus pascuali*, both in ventral view. × 1. Abbreviations: ca, concavity for acromion; c c, concavity for proximal end of the clavicle; dist, distal end of clavicle; f, ventral flange on distal end of clavicle; pr, posterior ramus of interclavicle; prox, proximal end of clavicle.

most prominent at their intersection. With the exception of the posterior part of the longitudinal ridge, which gradually fades out, the ridges become more salient toward the margins. There is no evidence that the longitudinal ridge was a deep keel as in *Exaeretodon* sp. (Bonaparte, 1963a). The posterior ramus in *M. pascuali* is similar in length and form to that in galesaurids, and is unlike the very short ramus of *Exaeretodon* sp.

The *Massetognathus pascuali* clavicle is robust. The proximal two-thirds are more or less straight (Fig. 5B), the distal third curving sharply posterodorsally. The broad, flat plate on the proximal end articulates with the previously described concavity (c c, Fig. 5A) in the interclavicle. Along the ventral aspect of the distal

third runs a flange (f, Fig. 5B) similar to that noted in African Triassic cynodonts (Jenkins, in press) and *Exaeretodon* sp. (Bonaparte, 1963a). This flange continues to the distal end where it contributes to the formation of a concavity (ca, Fig. 5B) for reception of the acromion. The clavicle is essentially identical to that in galesaurids.

The scapula, coracoid, and procoracoid in *Massetognathus pascuali* are firmly synostosed, although the joints can readily be distinguished (Fig. 6A). The scapular blade, elongate and narrow, bears a distinct concavity on its lateral surface—a fossa presumably for the supracoracoideus muscle, the infraspinatus homologue of mammals. The anterior margin of the blade is reflected sharply laterally, the posterior margin somewhat less so. An acromion process as such is not preserved on any of the scapulae; this absence may be due to postmortem damage to a delicate process or to the fact that the clavicular concavity simply fitted to the convex edge of the anterior scapular base (ac, Fig. 6A). The scapular half of the glenoid is a hemicircular and slightly convex facet that faces posteroventrally and somewhat laterally.

The coracoid is basically triangular in lateral view (co, Fig. 6A). The posterior end forms an elongate, attenuated process terminated by a tubercle for the origin of the coracoid head of the triceps (co tr, Fig. 6A). The process is morphologically similar to the same feature in *Pascualgnathus polanskii* and in African Triassic cynodonts, but differs in form from that in *Exaeretodon* sp. as interpreted by Bonaparte (1963a). Between the glenoid and the triceps tubercle, the superior margin of the coracoid is about 2 mm wide and is slightly concave from front to back. The slightly convex inferior margin is, in contrast, extremely thin bone, and, as a consequence, is invariably damaged postmortem. A saddle-shaped facet, concave dorsoventrally and convex transversely, constitutes the coracoid half of the glenoid.

The procoracoid (pr, Fig. 6A) appears to be an irregularly shaped, flat plate, but in no available specimen are the free margins complete. There are so many basic similarities in the scapulocoracoid of *Massetognathus pascuali* and African cynodonts that a complete procoracoid of the former would probably have the same oval shape characteristic of the latter. A crescentic depression on the lateral aspect along the inferior margin may represent the biceps origin. Above lies the round procoracoid foramen (f pr, Fig. 6A) sculptured in a ventrolateral direction to facilitate passage of its nerve and blood vessels. The evidence as to whether the procoracoid participated in the glenoid is equivocal. I

believe that the procoracoid probably supported articular cartilage at the very anterior extremity of the glenoid (see left glenoid, Fig. 6A), but there is no certainty of the procoracoid contributing to the shoulder joint as there is for some African Triassic cynodonts.

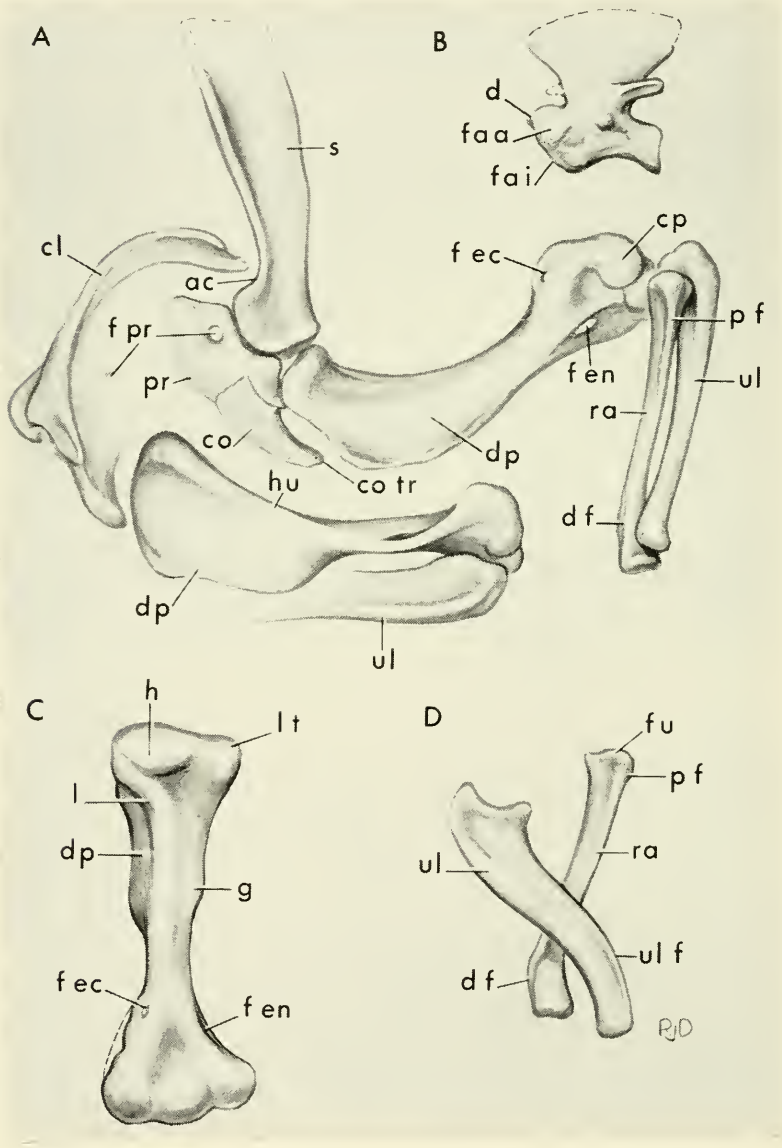

Figure 6. Elements of the postcranial skeleton of *Massetognathus pascuali*, drawn as preserved *in situ*. *A*, Incomplete left shoulder girdle and forelimbs seen from the left side. *B*, Lateral view of axis. *C*, Dorsal view of left humerus. *D*, Medial view of left radius and ulna. All × 1. Abbreviations: ac, area of clavicular articulation (distinct acromion process not developed); cl, clavicle; co, coracoid; co tr, tubercle for coracoid head of triceps; cp, capitellum; d, dens; d f, distal flange on radius; dp, deltopectoral flange; f a a, atlas centrum facet for atlas arch; f a i, atlas centrum facet for atlas intercentrum; f ec, ectepicondylar foramen; f en, entepicondylar foramen; f pr, procoracoid foramen; g, groove possibly representing teres major insertion or the origin of one of the humeral triceps heads; h, humeral head; hu, humerus; l, ridge possibly representing insertion of the teres minor; l t, lesser tuberosity; p f, proximal flange on radius; pr, procoracoid; ra, radius; s, scapula; ul, ulna; ul f, ulnar flange.

Forelimb

Principal characteristics of the humerus of *Massetognathus pascuali* are the relatively broad expansion of the proximal and distal ends, and the large deltopectoral flange. The proximal end of the shaft is bowed dorsally and the head is oriented to a more dorsal position. The well-rounded head (h, Fig. 6C) possesses greatest curvature along its dorsoventral axis. As preserved, the articular surface is confluent medially with the lesser tuberosity (l t, Fig. 6C) and laterally with the proximal margin of the deltopectoral flange. The greater tuberosity presumably arose in the mammalian lineage between the head and the proximal margin of the deltopectoral crest, but in *M. pascuali* there is no evidence of a distinct tubercle. The greatest width of the proximal end, from the lesser tuberosity to the region of the presumptive greater tuberosity, measures approximately one-third the total length of the humerus. The broad deltopectoral flange is slightly more than half the total length of the humerus. The free edge of the flange thickens and everts (laterally) at its proximal and distal extremities, but along the middle part is rather thin and flat. From the region of the presumptive greater tuberosity a low, bony ridge runs obliquely across the flange toward the shaft (l, Fig. 6C). An identical ridge on the humeri of certain African Triassic cynodonts has been interpreted as possibly representing the insertion of a teres minor (Jenkins, in press). On the posterodorsal aspect of the shaft is a groove possibly representing the insertion of the teres major or the origin of one of the humeral triceps heads (g, Fig. 6C); Bonaparte (1966b) interpreted a rugosity at this site in *Pascualgnathus polanskii* as the origin of the medial triceps head.

The distal end of the humerus is triangular in dorsal view, its maximum breadth being approximately 40 per cent of the humeral length. Arising from the robust ectepicondylar region, a thin supracondylar flange runs proximally as well as somewhat dorsally. The flange, pierced in its proximal half by a small ectepicondylar foramen (f ec, Fig. 6A, C), becomes a low crest at the middle of the shaft and is continuous with the ridge (l, Fig. 6C) described above. A stout bar of bone arising from the entepicondylar region encloses an elongate, oval entepicondylar foramen (f en, Fig. 6A, C). The capitellum (cp, Fig. 6A) is bulbous and contributes to the thickness of the ectepicondylar region. The trochlea immediately adjacent is a broad, shallow groove; the principal axis of this groove is dorsoventral, as expected, but it is also slightly oblique—the dorsal part being more laterally situated than the

ventral part. Morphologically, the humerus of *M. pascuali* is essentially identical to that in *Pascualgnathus polanskii* and galesaurids; apparent differences with galesaurids, e.g., the greater roundness of the head and capitellum, are due to the better ossification in *M. pascuali* and *P. polanskii*. As Bonaparte (1963a) noted, the humerus of *Exaeretodon* sp. is more similar to the dicynodont or gorgonopsid pattern than to that typical of galesaurids, and thus stands in contrast to the conventional cynodont humerus of *M. pascuali*.

The radius has a slight sigmoidal curvature (which facilitates its crossing over the anterior aspect of the ulna) and expanded proximal and distal ends. The nearly circular proximal articular facet forms a shallow concavity, in which the greatest curvature is anteroposterior (as is its reciprocal surface on the capitellum). On the posteromedial aspect of the proximal end is an excrescence that bears a facet (f u, Fig. 6D) apparently for articulation with the ulna. From this excrescence, a distinct flange (p f, Fig. 6D) runs distally to about the midpoint of the shaft. On better preserved material of African Triassic cynodonts, I interpreted a similar flange as possibly being associated with the biceps insertion and the radio-ulnar interosseous ligament (Jenkins, in press). Bonaparte (1963a) interpreted a similar feature in *Exaeretodon* sp. as marking the position of the interosseous ligament. The distal end of the radius expands gradually to the distal articular facet which is oval (long axis transverse) and shallowly concave. A distal flange (d f, Fig. 6D) arises near the midpoint of the shaft essentially as a continuation of the attenuating proximal flange described above. Beginning on the posterior aspect of the shaft, the distal flange takes a spiral course toward the lateral aspect as it enlarges distally. Its position is suggestive of the attachment of an intermuscular septum separating flexor and extensor muscle groups.

The ulna, like the radius, is sigmoidally shaped but is expanded only at its proximal end (Fig. 6D). The relatively shallow semilunar notch represents the typical cynodont condition—basically oval in outline, but with a rather straight medial margin and a nearly hemicircular lateral margin. An olecranon process is not present or at least was not ossified; the proximal end of the ulna, where such a process would be developed, is broad and rugose. The transversely narrow shaft of the ulna bears on its anteromedial aspect a flange (ul f, Fig. 6D) that extends from the semilunar notch to the distal articular facet. In all probability this flange represents the ulnar attachment of the interosseous ligament. The lateral surface of the shaft reveals one large, spoon-shaped fossa proximally, and on the medial surface two fossae, one proximal, the other distal. All three fossae are well represented in African

Triassic cynodonts, and I have proposed (Jenkins, in press) that they represent origins of various manual flexor and extensor muscles. The distal articular facet, convex from front to back, is broad anteriorly and narrow posteriorly and thus is triangular in outline. Both the radius and ulna of *M. pascuali,* as far as available material permits comparison, are extremely similar to their counterparts among galesaurids and in *Pascualgnathus polanskii.* Although definite similarities exist with the antebrachial elements of *Exaeretodon* sp., the essential identity of the *M. pascuali*-galesaurid pattern is incontrovertible.

Only an incomplete and disarticulated series of seven or eight carpals of *Massetognathus pascuali* is known, but these are so poorly preserved, and good comparative material is so scanty, that no constructive observations on the manus can be made at this time.

Pelvis

A complete pelvis of *Massetognathus pascuali* is not yet available, although enough is known of the ilium and ischium for preliminary description and comparison with other forms. The ilium bears an elongate, vertical blade, spatulate in front and lanceolate behind (il, Fig. 2). The lateral aspect of the blade is concave, especially anteriorly. The shape of blade, as well as the relative proportions of the pre- and postacetabular regions, is most similar to that in *Pascualgnathus polanskii* and is comparable to that of galesaurids, cynognathids, and diademodontids; *Exaeretodon* sp., on the other hand, has an iliac blade quite unlike the foregoing (Bonaparte, 1963a). The base of the iliac blade in *M. pascuali* is constricted into a short neck, below which are medial and lateral processes. The medial process (m p, Fig. 2B) bears two articular surfaces—one each for the pubis and ischium—which intersect at an angle of about 150°. The lateral process bears a nearly circular, concave facet that represents the iliac contribution to the acetabulum (a il, Fig. 2B). The facet is oriented principally in a posteroventral direction but with a slight lateral eversion.

Only the dorsal half of the ischium is available for examination (is, Fig. 2). The concave acetabular surface faces anterolaterally and is oriented essentially vertically. The postacetabular part of the ischium constitutes a broad plate that ventrally meets its counterpart of the opposite side. A longitudinal groove (gr, Fig. 2) on the dorsal margin of this plate terminates posteriorly at an ischial tuberosity (is t, Fig. 2).

Available pubes have been extensively damaged postmortem.

The pubic contribution to the acetabulum is considerably smaller than that of the ischium. Neither the obturator fenestra nor the ventral aspect of the pelvic basin is preserved.

The bony acetabulum is relatively shallow—a little more than 5 mm deep. The continuous, sharp rim around the acetabulum defines a more circular socket than that known in African Triassic genera. In all other details, the pelvis of *Massetognathus pascuali* appears to be morphologically similar to that in *Pascualgnathus polanskii,* galesaurids, and even larger African Triassic forms.

Hindlimb

The femur (Figs. 7, 8A) is a moderately slender bone, except for the expanded proximal end, which bears robust trochanters. The femoral head, bulbous and almost hemispherical as in mammals, is reflected medially but also somewhat dorsally by virtue of the dorsal bowing of the proximal end of the shaft (Fig. 8A). The protuberant trochanter major (tr mj, Figs. 7, 8A) measures about 5 mm in thickness. A pear-shaped area of smooth bone on its apex may represent the principal site of muscle attachment or of a subtendinous bursa. The bone surface immediately adjacent to the apex is rugose. The trochanter minor (tr mn, Figs. 7, 8A) forms an elongate flange that arises abruptly near the intertrochanteric

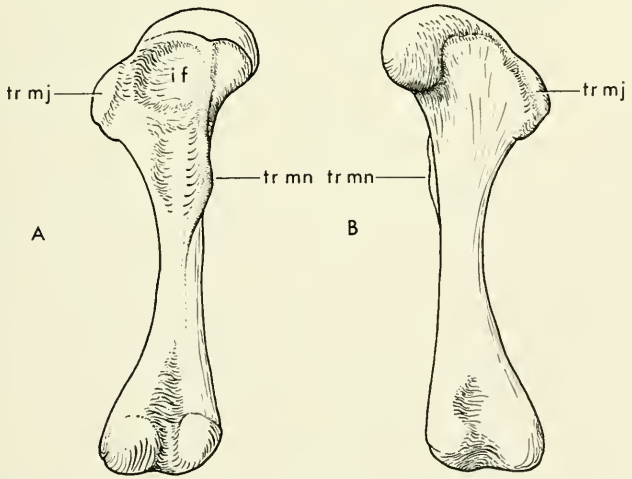

Figure 7. Reconstruction of a left femur in *Massetognathus pascuali* in *A*, ventral, and *B*, dorsal views. × 1. Abbreviations: i f, intertrochanteric fossa; tr mj, trochanter major; tr mn, trochanter minor.

fossa (i f, Fig. 7) and gradually disappears slightly distal to the shaft's midpoint. In cross-section, the middle of the shaft is essentially rectangular; its thickness from extensor (dorsal) to flexor (ventral) surfaces is about 6 mm, from the medial to lateral surfaces 4.5 mm. The distal end of the femur expands gradually but asymmetrically, the lateral condyle being broader and farther offset from the femoral axis than the medial. The medial condyle projects more ventrally than does the lateral condyle. The fibula appears to have articulated on the lateral epicondylar region where a shallow groove (f f, Fig. 8A) occurs. The femur of *Massetognathus pascuali* is morphologically comparable to the femora of *Pascualgnathus polanskii* and even the larger African genera in which ossification of the extremities was well developed (Jenkins, in press). In smaller forms, such as galesaurids, the femur appears to be different because of the lack of ossification of the extremities and trochanters.

The tibia is a transversely slender bone, bowed somewhat anteriorly. The two proximal articular facets, oval in outline and shallowly concave, are separated by a low, median ridge. The

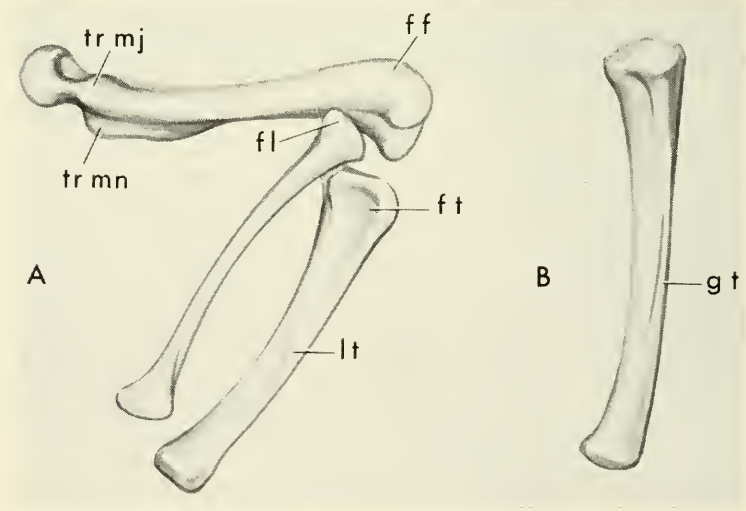

Figure 8. Elements of the hindlimb of *Massetognathus pascuali*, drawn as preserved *in situ*. *A*, Right femur, tibia and fibula in lateral view. *B*, Left tibia in medial view. All × 1. Abbreviations: f f, facet for articulation with fibula; fl, fibular flange for femoral articulation; f t, lateral tibial fossa of uncertain significance; g t, groove on medial aspect of tibia; l t, lineation on lateral aspect of tibia; tr mj, trochanter major; tr mn, trochanter minor.

lateral margin of the lateral facet is thickened and protuberant, and it appears likely that part of the proximal fibula articulated here. On the proximal end of the lateral aspect of the shaft is a deep fossa (f t, Fig. 8A) of uncertain significance; from the posterior margin of this fossa a faint lineation (l t, Fig. 8A) runs obliquely across the shaft to merge with the narrow anterior margin of the shaft. Also of uncertain significance is a slightly curved groove (g t, Fig. 8B) along the middle of the shaft's medial aspect. The distal extremity of the tibia has a marked lateral expansion that sufficiently widens at the terminus to accommodate a broad, slightly convex facet for the astragalus.

The fibula, a very slender-shafted bone with enlarged extremities, is bowed laterally. The shaft appears to have been wider transversely than anteroposteriorly. On the one complete specimen, a shallow groove running the length of the shaft along its medial aspect can be detected. A flange on the proximal end (fl, Fig. 8A) probably contacted a groove on the lateral epicondylar region of the femur; the remainder of the proximal fibula articulated with the tibia. The distal end, like the proximal, broadens anteroposteriorly and is inflected somewhat medially. All features of both tibia and fibula found in *Massetognathus pascuali* are duplicated in galesaurids and even in the larger African Triassic genera. The tibia and fibula of *Exaeretodon* sp., by contrast, depart from the uniform pattern of other cynodonts by being proportionally more massive.

Nothing can be described of the pes of *Massetognathus pascuali* from the available material.

Discussion

Massetognathus pascuali, about 50 cm in length from head to tail, was a cynodont of relatively slender build (Fig. 9). The shortness of the limbs relative to the approximated trunk length gives the body a "low-slung" appearance. The head seems disproportionately large for the body, but a relatively massive head is a common cynodont characteristic.

The postcranial skeleton of *Massetognathus pascuali* is basically like that in galesaurids, diademodontids, cynognathids and *Pascualgnathus polanskii.* Limited morphological diversity appears to be the rule for the postcranial skeletons of Triassic cynodonts. *Exaeretodon,* however, is an exception; the postcranial skeleton in this genus differs in major details from the pattern characteristic of other Triassic cynodonts. Bonaparte (1963a) recognized postcranial specializations in his original description and implied that

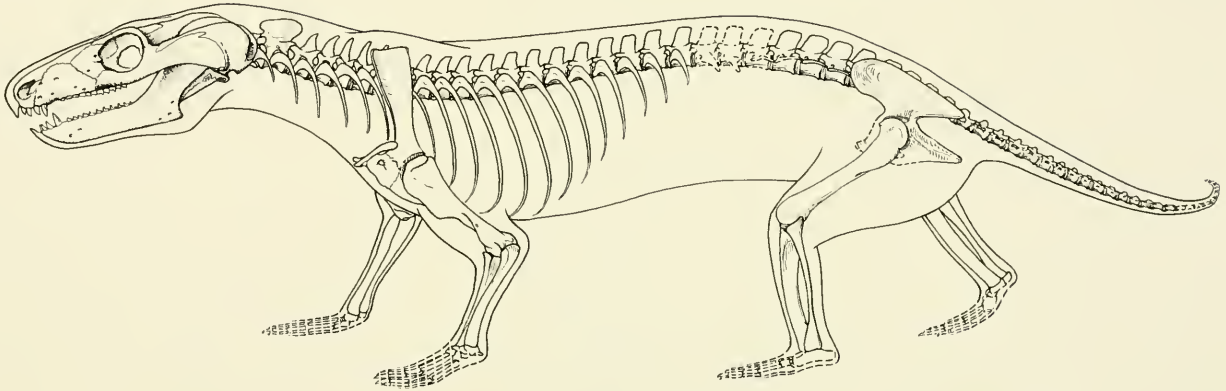

Figure 9. Skeletal reconstruction of *Massetognathus pascuali*, ⅓ natural size. Skull modified after Romer (1967). Dashed lines indicate areas of uncertain morphology.

similar features might also be characteristic of other traversodontids. From similarities between the genera *Exaeretodon* and *Leavachia,* Bonaparte further inferred that traversodontids possibly evolved from procynosuchids in a lineage separate from that giving rise to other cynodont families. These conclusions, credible on evidence available in 1963, now require modification, because *P. polanskii* and *M. pascuali* demonstrate that *Exaeretodon* is a specialized traversodontid. Such specialization is not surprising in view of the fact that this genus lived later in the Triassic than any form with which it has been compared. Limb bones in *Exaeretodon* sp. are more robust than in other cynodonts (Fig. 10), no doubt in relation to its unusually large size. Some *Exaeretodon* features are unknown in other cynodonts. For example, a deep, sagittal keel occurs on an unusually short interclavicle; an extra trochanteric process runs distally from the trochanter major along the ventral aspect of the femur (Bonaparte, 1963a; a similar process, identified as a trochanter minor by Parrington (1961), is known in a whaitsid therocephalian and in a scaloposaurid bauriamorph). Furthermore, the lack of rib specialization is a unique feature for a Triassic cynodont. Thus, as a specialized traversodontid, *Exaeretodon* is no longer as relevant to the problem of traversodontid origins as it was when other traversodontid genera were poorly known.

Two facts bear on the problem of traversodontid origins. First, morphological similarities between the postcranial skeletons of *Massetognathus pascuali, Pascualgnathus polanskii,* and African Triassic cynodonts are evidence of close phylogenetic relationship. Similarities between the skull and specialized ribs of *P. polanskii* and *Diademodon* (see Bonaparte 1966b) raise the likelihood that traversodontids and diademodontids were derived from a common stock. Second, the paucity of information available on the procynosuchid postcranial skeleton does not appear to be useful in evaluating relationships with other cynodont families. Bonaparte (1963a) compared the postcranial morphology of *Exaeretodon* sp. and *Leavachia duvenhagei* and on this basis suggested the possibility that traversodontids and procynosuchids were directly related. The difficulty of this approach may be illustrated with respect to the forelimb in which, for example, Bonaparte noted similarity between the radius and ulna of *Exaeretodon* sp. and *L. duvenhagei.* The radius and ulna of *L. duvenhagei* are, in fact, poorly known and in relative proportions do not resemble those in *Exaeretodon* sp. more than those of African Triassic cynodonts (Fig. 10). Similarities cited by Bonaparte between the manus of *Exaeretodon* sp. and

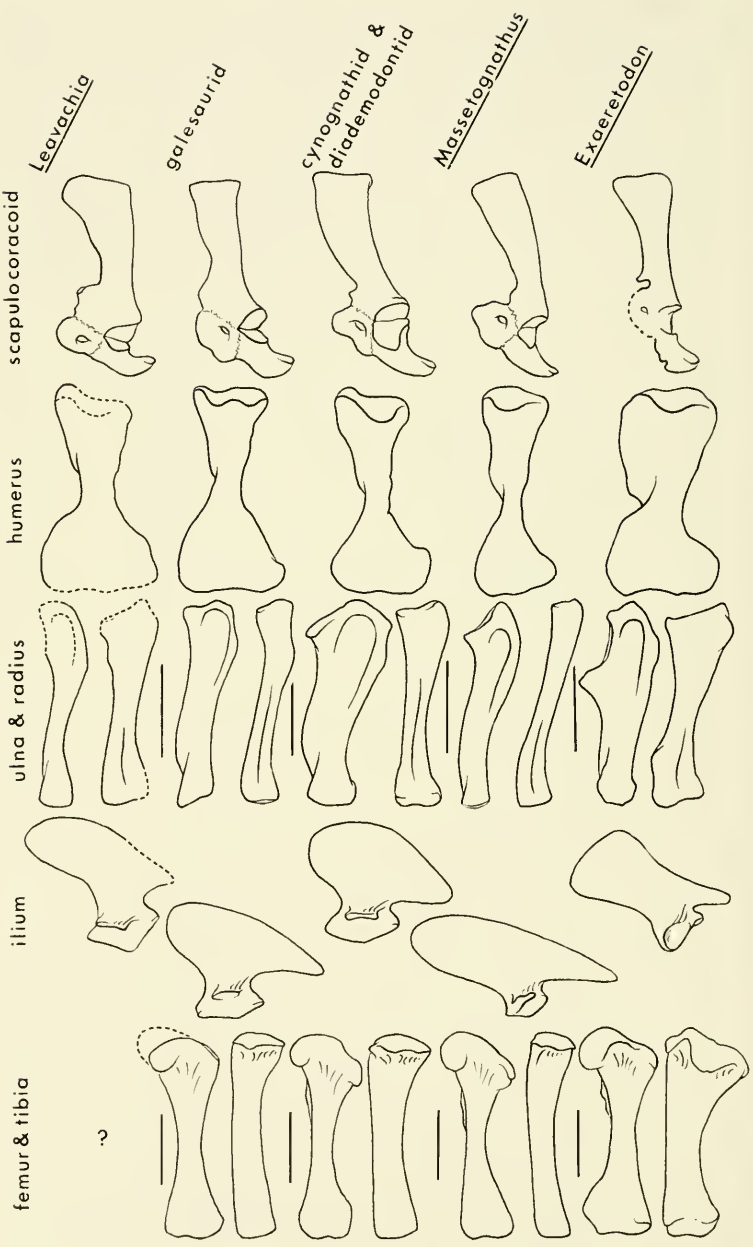
Leavachia
galesaurid
cynognathid &
diademodontid
Massetognathus
Exaeretodon
scapulocoracoid
humerus
ulna & radius
ilium
femur & tibia
?

Figure 10. Diagrammatic comparison of postcranial bones in various major groups of cynodonts. *Leavachia*, in part modified from Broom (1948) and in part drawn from stereoscopic photographs, represents Procynosuchidae. The galesaurid and cynognathid–diademodontid patterns are taken from Jenkins (in press); cynognathids and diademodontids are sufficiently alike in their postcranial morphology to be represented here by a single pattern. The *Exaeretodon* material is drawn from Bonaparte (1963b). All bones have been reduced to a standard dimension to illustrate proportional differences.

L. duvenhagei are of equivocal significance in view of the almost total lack of information on the manus of other cynodonts. Bonaparte's contention that the humeri of *Exaeretodon* sp. and *L. duvenhagei* are proportioned alike is valid, but the dissimilarity to those in other cynodonts is not so great as to make this comparison especially significant (Fig. 10). Bonaparte admitted that the scapulocoracoid of *Exaeretodon* sp. is more like that in *Cynognathus* sp. than that in *L. duvenhagei*. This resemblance, in Figure 10 at least, is not particularly marked, although the specialized character of the scapulocoracoid in *Exaeretodon* sp. is evident. Thus, comparisons between forelimb features of several cynodont families provide no evidence of special affinity between traversodontids and procynosuchids.

The iliac blade of *Massetognathus pascuali* has a long posterior process like that in African Triassic cynodonts (Fig. 10) and *Pascualgnathus polanskii*. In contrast, the same process in *Exaeretodon* sp. is relatively short (Fig. 10), and as a consequence the blade as a whole has a more mammalian shape (Bonaparte, 1963a). The iliac blade in the type of *Leavachia duvenhagei* appears to have a short posterior process (Fig. 10; Broom, 1948) but also appears to be somewhat damaged. Thus a long posterior process may have existed in procynosuchids, and on present evidence, at least, the ilia of *Exaeretodon* sp. and *L. duvenhagei* do not indicate special affinity between the two.

Bonaparte (1963a) cited the absence of specialized ribs in *Exaeretodon* sp. and *Leavachia duvenhagei* as possible evidence of a close relationship between traversodontids and procynosuchids. The subsequent discovery of specialized ribs in *Massetognathus pascuali* and the reclassification of *Pascualgnathus polanskii* (which has specialized ribs of the *Diademodon* pattern) make this observation no longer significant. It is interesting, however, that in the type of *Leavachia duvenhagei* (Rubidge Collection No. 92, Graaf Reinet, South Africa) the last dorsal rib appears to be laterally oriented (Fig. 4C), much as in *M. pascuali* and in other cynodonts with specialized ribs. On the dorsal aspect of the shaft is a ridge (b, Fig. 4C) comparable in position and orientation to a similar ridge in *M. pascuali*, cynognathids, and diademodontids (b, Fig. 4A, B). Furthermore, Konjukova (1946) figured a specimen of the procynosuchid *Permocynodon*, incompletely prepared from the ventral aspect. The posterior dorsal ribs are directed anterolaterad (as in *Thrinaxodon*, for example) and the shafts appear to be wider than those of more anterior dorsal ribs. The capitular articulations of posterior dorsal ribs in *Permocynodon* are relatively broad, a feature typical of cynodonts in which the posterior dorsal

ribs are synostosed. On this incomplete evidence, it appears possible that rib specialization was already underway in procynosuchids and was further modified in the various cynodont families descended from them.

Hopson and Crompton (1969), in a discussion of the origin of mammals, observe that galesaurids such as *Thrinaxodon liorhinus* would be ideal candidates for mammalian ancestors were it not for the presence of specialized ribs. These authors suggest that *Exaeretodon* is relevant to this problem because its nonspecialized ribs may represent a reversion from a specialized pattern, and similar trends may have occurred in galesaurids. There is now substantial evidence favoring the view that rib specialization was gradually lost in traversodontids. *P. polanskii,* the earliest traversodontid for which ribs are known, has a costal morphology of a *Diademodon* pattern. *M. pascuali,* temporally intermediate between *P. polanskii* and *Exaeretodon* sp., has ribs with less extensive specialization. Thus the ribs of *Exaeretodon* sp. apparently represent a reversion to a nonspecialized condition, and are not primitively nonspecialized as originally suggested by Bonaparte (1963a). That such a loss occurred in one family of cynodonts increases the possibility that a similar reversion occurred in advanced galesaurids—or their descendants—during the reptile–mammal transition.

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I am grateful to Professor Alfred S. Romer of Harvard University for enabling me to participate in the Chañares faunal studies. Professor Romer, together with Professor Rosendo Pascual, Universidad de la Plata (Argentina), generously consented to my request to describe *Massetognathus pascuali* as a sequel to my work on African cynodonts. Professor Romer furthermore provided preparational facilities and staff, skillfully supervised by Mr. Arnold D. Lewis, with the result that the material was presented to me in excellent condition. Dr. José F. Bonaparte of the Instituto Miguel Lillo de Tucumán (Argentina) kindly read the manuscript and clarified several important points of cynodont anatomy and relationships. Figures 6 and 8 were prepared by Mr. Robert J. Demarest. I thank Dr. James A. Hopson of the University of Chicago for making available his collection of stereoscopic photographs of *Traversodon,* and Dr. James Kitching of the Bernard Price Institute for Palaeontological Research (Johannesburg) for verifying some features on a specimen of *Leavachia.*

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BREVIORA

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Anolis jacare Boulenger, a "solitary" anole from the Andes of Venezuela

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Carlos Rivero-Blanco[3]

ABSTRACT. *Anolis jacare* Boulenger is the sole member of its genus in the Andes of Mérida in Venezuela. In external morphology, size, and to some extent in behavior, it resembles its congeners on the one anole islands of the Lesser Antilles. The karyotype of *A. jacare*, however, demonstrates that it is not closely related to either of the two Lesser Antillean stocks which it resembles and these we know not to be closely related to each other. The similarity of *A. jacare* to the two Lesser Antillean stocks and of these to each other seems to be due to selection for a similar ecological type.

In 1903 Boulenger described *Anolis jacare* from several specimens in a collection made by S. Briceño at Mérida, Venezuela, at an elevation of 1600 meters. As all too frequently happens in Boulenger's work, the description was altogether without comparison or note on relationship.

Since its description additional specimens have been taken, all in the Venezuelan Andes, but there has been little discussion of the species. There has never been any question of its validity.

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Schmidt (1939: 9) mentioned a peculiar feature of the species, the double row of keeled scales forming the dorsal caudal margin. This is a feature which *A. jacare* shares with some South American species and with the very distantly related *A. barkeri* of Mexico. In 1960 Etheridge placed *jacare* in the *latifrons* series of his alpha section of the genus *Anolis*. This section, distinguished by the absence of transverse processes on the caudal vertebrae, represents an old endemic South American stock, which today shares South America with more recent (beta section) invaders from Central America.

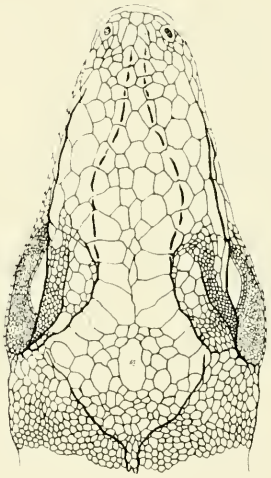

Figure 1. *Anolis jacare*. Dorsal view of head. AMNH 13444.

No previous mention of *A. jacare* has cited its most interesting feature: alone of native South American species, it shows a close resemblance to West Indian species, specifically those of the Lesser Antilles. In fact, its resemblance to *Anolis leachii*, except in size, is such that even an experienced student of *Anolis*, presented with a specimen of *jacare* without locality, is very likely to confuse it with *A. leachii*.

Table 1 compares *A. jacare* to *A. leachii* and to the Leeward Island species more similar in adult size, *A. marmoratus*.

When *A. jacare* is closely examined, of course, there should be no real possibility of confusing it with *A. leachii*. The dorsal squamation of the tail, larger dewlap, relatively larger ventrals, smaller scales on the snout, etc., permit easy recognition of *A.*

jacare. On general appearance, however, relationship will still seem plausible.

However, in terms of geography, close relationship of *jacare* of the Andes of Venezuela and *leachii* of the northern Lesser Antilles is *prima facie* unlikely. In addition, there is good evidence that the *bimaculatus* group (Gorman and Atkins, 1969) is derived from the still more distant Puerto Rican stock and that it is to this Puerto Rican stock or a still more primitive group that any phyletically meaningful resemblance would be expected.

Geographically, the *roquet* group in the southern Lesser Antilles would be a little more plausible as close relatives of *jacare* than the *bimaculatus* group. Gorman and Atkins (1969) have commented on the close external resemblance of the *roquet* and *bimaculatus* groups. Earlier, Underwood (1959) was able to find only the most trivial scale differences between the two groups. However, on all the characters by which Underwood was able to separate the *roquet* and *bimaculatus* groups, *jacare* fits the *bimaculatus* group.

With the eight Venezuelan species geographically closest, *jacare* shows little similarity. (None of the eight appear to overlap the distribution of *jacare* at all.) Five of the eight (*chrysolepis, auratus, fuscoauratus, tropidogaster, biporcatus*) belong to the beta division of Anolis (Etheridge, 1960) and are neither osteologically nor in squamation close to *jacare*. The three remaining species (*squamulatus, punctatus, tigrinus*) are referred by Etheridge (1960) to the same group as *jacare* (the *latifrons* series of the alpha section of *Anolis*). However, these again show no evidence of close relationship. *Squamulatus* and *tigrinus* are very different from *jacare* in size (*squamulatus* a giant, *tigrinus* a dwarf), and *punctatus* is conspicuously specialized in the swollen snout of the male. All differ significantly from *jacare* in scale characters.

There are indeed no South American or other continental species to which A. jacare *shows important resemblances.* We are left, therefore, with the external similarities to the *bimaculatus* species group and, less marked, to the *roquet* species group. If these resemblances go deeper, we appear to be faced with a zoogeographic puzzle which may need a difficult and complex solution.

It has seemed worthwhile, therefore, to broaden the study of *A. jacare* to include such more recently utilized characters as karyotype and ecology. The remainder of this paper deals with the results of these analyses.

Chromososome analysis (O. A. Reig and P. Kiblisky):

Four male and three female individuals have been worked for chromosome analysis. Our report is based on the four male individuals. We failed to get results with one of the females, and the other two were sent to Dr. George Gorman, who, by the use of a blood culture microtechnique, obtained a chromosome count agreeing with our results (personal communication). The male specimens have been deposited in the Collection of Herpetology of the Museum of Natural History of Caracas (MCNC 5601-5604). Those studied by Dr. George Gorman are in the Museum of Vertebrate Zoology, University of California.

Our animals were injected with 0.5 cc Colchicine Merck (solution 5 mg per cc) 2–3 hours before killing. Testes were removed, minced with scalpel, and pretreated for 20 minutes in a hypotonic solution of sodium citrate 0.7%. The material was centrifuged at 800 rpm and the pellet resuspended in 3/1 alcohol-acetic fixative. After a new centrifugation, the pellet was changed to 2/1 fixative. Spreads were obtained by air-drying on chilled slides or by squashing, then stained with acetolactic orcein, Giemsa and Feulgen, and mounted in Canadian balsam. Chromosomes were observed with a Wild M-20 microscope, and each appropriate metaphase or meiotic prophase was recorded and sketched. Numerous additional cells were also counted and observed. Selected cells from those recorded were photographed with high contrast Copy Kodak film, and karyotypes were constructed from enlarged prints. A total of 50 cells was recorded, as listed below:

	Spermatogonial metaphases	*Diakineses*	*Metaphases II*
Specimen Nr. MCNC 5601	9	3	—
Specimen Nr. MCNC 5602	4	1	1
Specimen Nr. MCNC 5603	15	1	—
Specimen Nr. MCNC 5604	13	3	—
All specimens	41	8	1

Results

The diploid chromosome complement of *Anolis jacare* is composed of 32 chromosomes (Figs. 3 and 4). Of them, 12 are macrochromosomes and 20 are microchromosomes. The diakineses (Fig. 5) show six large bivalents and ten very small bivalents. Chromosome number and structure are identical in all the studied specimens. The six pairs of macrochromosomes do not gradually

decrease in size but can be divided into three groups (Fig. 1). Group A is formed by three pairs of large metacentric and submetacentric chromosomes. (In the following, we use the nomenclature proposed by Levan, Fregda, and Sandberg, 1964.) Pair A-1 comprises *sm* chromosomes, whereas pairs A-2 and A-3 are *m*-chromosomes. Chromosomes of pair B-1 are around 4/5 the length of those of pair A-3. Pairs B-1 and B-2 are easily distinguishable in size. Group C comprises one pair of small *st* chromosomes ($r = 3.66$), clearly smaller than those of pair B-2 and three times larger than the largest chromosome of the set of the microchromosomes. A small difference in size and arm ratio was found in the chromosomes of this pair in all the cells where the shape of these chromosomes was clear enough, so that the pair might tentatively be considered as heteromorphic. Whether or not the presumptive heteromorphic pair is to be interpreted as an X-Y sexual system cannot be solved in the absence of good female metaphases. In two of the chromosome spreads obtained by Gorman, the female karyotype also shows heteromorphism in this pair. Moreover, the ring-shaped form of the corresponding bivalent in male diakinesis does not seem to fit with the X-Y hypothesis. The 20 pairs of microchromosomes steadily decrease in size and seem to have terminal (*t*) or subterminal (*st*) centromeres.

Gorman (1965), Gorman and Atkins (1967, 1968a) and Gorman, Atkins and Holzinger (1967) have demonstrated that a karyotype of six pairs of macrochromosomes and twelve pairs of microchromosomes is shared by most of the studied species of iguanid lizards, including the anoles of the alpha group of Etheridge (1960) other than those of the *bimaculatus* series. The anoles of the beta group of Etheridge depart from this "standard" iguanid karyotype in showing seven pairs of macrochromosomes and a variable number of microchromosomes. Within the alpha group, the species of the *bimaculatus* series known in chromosome constitution (*bimaculatus, leachii, gingivinus,* and *marmoratus*) (see Gorman, 1965; Gorman and Atkins, 1966) are peculiar in having quite another kind of karyotype. In these species there is no sharp distinction between macro- and microchromosomes. There are from 18 to 20 chromosomes gradually decreasing in size that continue in five or six pairs of dotlike microchromosomes.

Anolis jacare departs from both the beta anoles and alpha anoles of the *bimaculatus* series in retaining the "standard" set of six pairs of macrochromosomes, easily distinguishable from the

microchromosome set. The morphological similarities referred to above with members of the *binaculatus* series are thus not supported by chromosome evidence, but this evidence agrees with the osteological evidence in indicating that this species belongs to the alpha group. Within the non-*binaculatus* series alpha anoles so far known in chromosome structure, however, a considerable variation occurs in details of structure of the macrochromosome set and in the number of microchromosomes. *Anolis roquet, equestris, carolinensis,* and *cybotes* are different from *Anolis jacare* in showing 22 or 24 microchromosomes and a steady decrease in size of the macrochromosomes, the only distinguishable break in size in these being between the fifth and the sixth pairs. *Anolis cooki, pulchellus, cristatellus* and *scriptus* of the *cristatellus* series (Gorman, Thomas, and Atkins, 1968) show the two sharp breaks in the macrochromosomes that are also observed in *A. jacare,* but in them the second break falls between the fourth and the fifth pairs instead of between the fifth and the sixth pairs as in *A. jacare.* In addition, those species of the *cristatellus* series mentioned above have heteromorphic sex chromosomes and only from 15 to 18 microchromosomes. *A. trinitatis* and *A. aeneus* of the primitive *latifrons* series agree with *A. jacare* in the two size discontinuities among the macrochromosomes. They have, however, 24 and 22 microchromosomes respectively, and the first break in the macrochromosomes falls between the second and the third pair. Moreover, the first pair of macrochromosomes is metacentric in all the illustrated karyotypes of alpha anoles, whereas it is submetacentric in *A. jacare.*

Anolis jacare thus seems to be an isolated species within the alpha group on the basis of the pattern of the size discontinuities among the macrochromosomes and the unique number of 20 microchromosomes. It is suggestive that a distinction of three groups within the macrochromosomes falling in the same order as in *A. jacare* can also be observed in the species of the beta anoles of the *grahami* and *chrysolepis* series so far reported (Gorman, 1965; Gorman and Atkins, 1967). There is, however, a sharp difference between the macrochromosome set of these species and that of *A. jacare*: in the former the group C comprises two pairs instead of one pair as in the latter, the number of pairs of macrochromosomes thus amounting to a total of seven, as in all of the beta anoles.

Given the widespread occurrence of six pairs of macrochromosomes in alpha anoles and most iguanids, we are inclined to evaluate differences in number of the macrochromosome set as more important than structural rearrangements within this portion of the karyotype. For this reason, and because *A. jacare* is clearly an alpha *Anolis* on osteological grounds, the similarities it shows with some of the beta anoles in chromosome structure are better interpreted as a departure from the "standard" iguanid karyotype that converged with some of the modifications shown in the anoles of the *grahami* and *chrysolepis* series. Admittedly, the amount of this convergence may be considerable. It would be possible to derive the karyotype of *A. jacare* from that of *A. chrysolepis* by centromeric fissions in the last pair of macrochromosomes of the latter, leading to two pairs of microchromosomes with terminal centromeres. This process would result in a complement with six pairs of macrochromosomes separable into three distinct groups, and in ten pairs of microchromosomes, exactly as in *A. jacare*. The osteological evidence, however, does not support any close relationships between these two species.

The chromosome analysis thus indicates that *Anolis jacare* is an alpha *Anolis* that has departed significantly from other members of this group in chromosome number and structure, though maintaining the standard iguanid karyotypic feature of six pairs of macrochromosomes.

Observations in life (C. Rivero-Blanco and E. E. Williams):

Since no information of any ecological sort had ever been provided for *Anolis jacare,* it was as important an objective of the expedition to Mérida to provide this information as to obtain chromosome data.

Only twelve anoles were collected during a period of three days of active search. All were obtained on medium and large-sized trees bordering the small Rio Milla just outside the city of Mérida (1639 meters above sea level). Several other areas within and outside the city of Mérida were carefully examined.

The general area is classified as Premontane Humid Forest in the scheme of L. R. Holdridge (J. J. Ewel and A. Madriz, 1968). The mean annual temperature is 19.1° C and the annual rainfall 1791 mm.

The two actual collection sites (Fig. 2) were roadside localities and were subject to more or less penetration by the sun, especially so in site 1 where trees were partly separated, less so in site 2 where the canopy was closed. In the first site, the anoles were

seen and collected on the branches of "majagua" (*Heliocarpus popoyensis,* Tiliaceae) and "guamo" (*Inga* sp., Leguminosae), at the second on "anime" (*Montanea quadrangularis,* Compositae) and on a very large tree 10–15 meters high, not identified, since leaves and flowers were not collected.

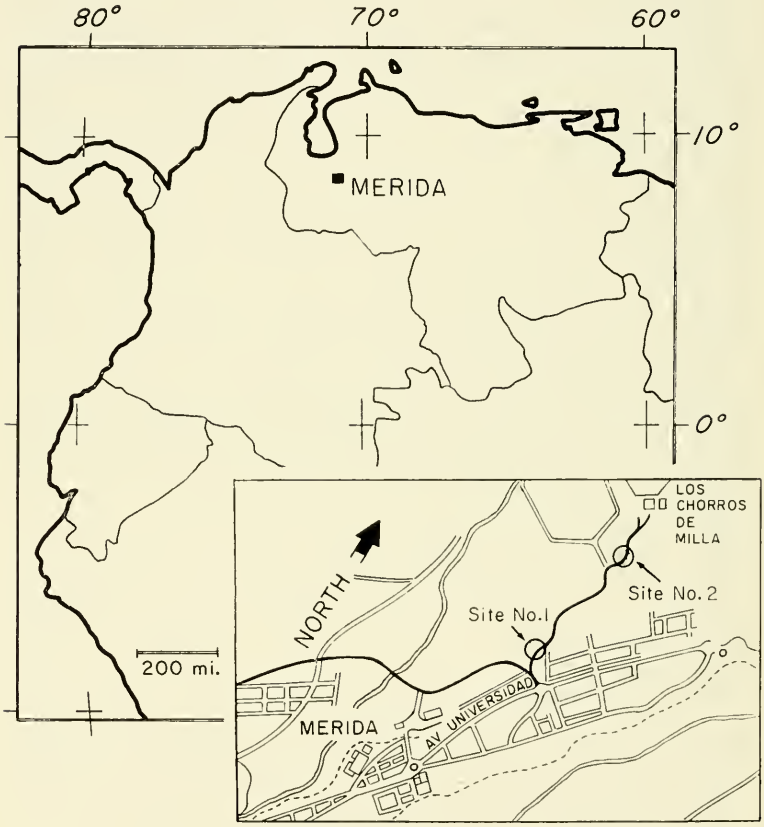

Figure 2. Map of the collecting sites for *Anolis jacare* along the Rio Milla outside Mérida.

Collecting was done with the aid of a 5 meter long telescopic fishing rod with a nylon noose. The animals were not shy but avoided the noose by moving around the branch or further along the branch or to other branches along the trunk or out on the finer twigs. Two escaped high into the canopy; others did not move at

all. The number of animals seen varied from none on many trees to four on one guamo tree. Few of those seen escaped the noose.

We have no belief that we have even the beginning of knowledge of the population density of this species. The animals were difficult to see and commonly lay along branches, and only twice were they seen on the main trunk of the trees. They obviously ranged widely within the trees they inhabited, including very high in the crown. The first specimen taken came from a guamo tree that was examined several times every day and even one night. It was this tree that, on the last afternoon, provided three additional animals to give a final result of two males and two females on a tree no more than six meters high and not especially complex. This result was possible only because, during the last afternoon, we had the help of a young local boy who was an excellent climber and who was able to spot from a higher position animals that could not be seen from below because of their resting position on branches.

In summary, this is an animal inhabiting primarily the crown and its branches, though not avoiding the trunk. It is not restricted to shade; several individuals seen were in partial sun or moved into sun without reluctance. It has no evident competitors. No other lizards were seen in the collecting area either on the trees or on the ground. Elsewhere in the vicinity other lizards were found: *Polychrus,* in a hedge, and *Ameiva* and *Cnemidophorus,* on the ground.

Discussion (E. E. Williams):

The karyotypic evidence clearly demonstrates a strong separation between *jacare* and either of the stocks of Lesser Antillean anoles. Equally there is sharp difference between *jacare* and the few mainland alphas that have been studied thus far (Gorman, personal communication). On the face of the evidence, *A. jacare* seems to occupy a rather isolated phyletic position.

It may be of interest and importance here that *A. jacare* is distributionally isolated also and that, very unusually for South American anoles, it is not known to be sympatric with any congeners in any part of its known range.

There are other South American species that extend beyond the range of their congeners somewhere at the periphery of their range. *A. jacare* is special in that so far as known its whole range is outside contact with any other anole.

Recent studies by T. Schoener (1970) have shown that in the Lesser Antilles, "solitary" species, i.e., species without sympatric

congeners, tend to be very similar in size and habitus. There also appears to be a broadened unspecialized ecology characteristic of these "solitary" anoles. We have noted above that the *bimaculatus* and *roquet* species groups are extraordinarily similar in scale characters. We emphasize now that they are so in spite of the fact that they are products of two quite separate invasions of the West Indies and are very distinct in karyotype and biochemistry.

Schoener infers, and we may agree with him, that some common selective factor must be at work to keep (or evolve) external similarity when wide underlying differences exist. That common selective factor would appear to be the negative one of the absence, or extreme limitation, of the number of congeners.

Certainly on the larger islands of the Greater Antilles a contrary rule exists: syntopic anoles are very diverse in morphology or size or both.

The modification of a species in the absence of congeners or other competitors in its general niche is sometimes spoken of as "release." In morphology, at least, it is proper to speak of a more positive selection than that implied by that essentially negative term. A certain size seems clearly optimal and presumably the features of squamation must likewise be held under selective control.

In ecological behavior, "release" seems a more descriptive term, since the wider range of habitat permitted a species in the absence of close competitors concords better with our intuitive sense of the meaning of release.

In the Lesser Antilles, there is often only one species per island and, except for instances of very recent importation and their very local occurrence (e.g., *wattsi* on St. Lucia, Underwood, 1959, 1962), there is a maximum of two species per island. These are relatively old islands and the species on them are well differentiated. They afford the classic and best examples of "solitary" anoles.

A. jacare, however, is as isolated in the Andes of Mérida as the solitary anoles of the Lesser Antillean islands. It is effectively on a mainland island; it is interesting therefore, but not unexpected, however, to find it resembling and behaving like an island anole—a solitary anole of an old small island.

The resemblances, then, of *A. jacare* to *A. leachii* or *A. marmoratus* are to be explained in terms of adaptation to similar selective pressures. We need not, in fact, seek any complex zoogeographic solution to the similarity of one anole on island mountains

to one on a distant island; the similarity is non-phyletic, strictly convergent.

TABLE 1

	jacare	*leachii*	*marmoratus*
snout-vent length of adult ♂	73 mm	96 mm	77 mm
scales across snout	6-8	4-5	4-5
scales between semicircles	0-2	0-1	0-1
loreal rows	4-5	4-5	4-5
scales between interparietal and semi-circles	1-3	1-2	1-2
supralabials to center of eye	6-9	7-8	7-8
mental	*not* deeper than wide	*not* deeper than wide	deeper than wide
number of sublabials in contact with infralabials	3-5	2-4	2-4
scales between sublabials in contact with mentals	4	4-6	3-4
ventrals	smooth	smooth	feebly keeled
lamellae under phalanges ii and iii of fourth toe	19-25	26-32	24-30
tail	compressed but without crest, 2 dorsal rows	compressed, with strong crest in males	Compressed, with weak dorsal crest in males
dewlap	large	small	large
color	green with variable dark vermiculations	green with dark vermiculations but these stronger on head than on body	green with light vermiculations on head in males only

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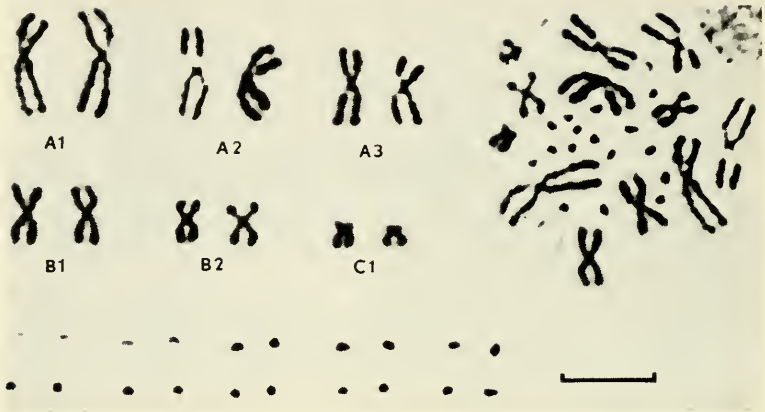

Figure 3. Spermatogonial metaphase and karyotype of *Anolis jacare*. Specimen no. MCNC 5601, cell no. A-167 T5 C2. Scale: 10 micra.

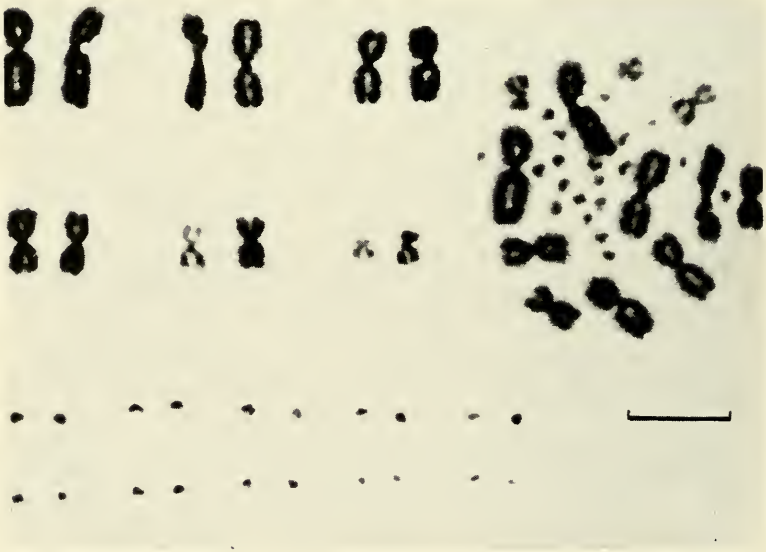

Figure 4. Spermatogonial metaphase and karyotype of *Anolis jacare*. Specimen no. MCNC 5604, cell no. A-171 T3 C2. Scale: 10 micra.

Figure 5. Diakinesis of *Anolis jacare*. Specimen no. MCNC 5603, cell no. A-170 T7 C1.

Figure 6. Rio Milla, Merida (site 1 of Fig. 2). To the right of the light post is the guamo (*Inga* sp.) in which two males and two females were collected. The other trees to the right are majagua (*Heliocarpus popayensis*) where other specimens were collected

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TAXONOMIC AND ECOLOGICAL NOTES ON SOME MIDDLE AND SOUTH AMERICAN LIZARDS OF THE GENUS *Ameiva* (TEIIDAE)

Arthur C. Echternacht

ABSTRACT. The taxonomy of two Middle American and one South American *Ameiva* (Sauria, Teiidae) is discussed. *Ameiva festiva niceforoi* Dunn is accorded species rank, *A. f. miadis* Barbour and Loveridge is formally designated a subspecies of *A. undulata*, and *A. undulata thomasi* Smith and Laufe is placed in the synonymy of *A. chaitzami* Stuart. Diagnoses and statements of range are provided for each, and ecological information is presented for *miadis*. The condition of the median parietal (divided or not) is shown to be unstable in *Ameiva* and useless for diagnosing species in Middle America.

INTRODUCTION

In the course of my studies of geographic variation in the Middle American species of the lizard genus *Ameiva*, I have found that certain taxa require reallocation and that diagnoses presented with the original descriptions of some are either in error or misleading. It is the purpose of this paper to clarify the taxonomic positions of three of these taxa. A diagnosis is presented for each, and ecological information is included where warranted.

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Ameiva niceforoi Dunn

Ameiva festiva niceforoi Dunn, Notulae Naturae no. 126: 1-2, 1943 (Holotype: ANSP 24300. Type Locality: "Sasaima, in the eastern Andes, 75 km northwest of Bogotá, altitude 1200 meters," Colombia. Collector: Hermano Niceforó Maria).

Diagnosis. *Ameiva niceforoi* can be distinguished from its congeners by the following combination of characters: Small size (maximum observed snout-vent length [SVL] 82 mm for males, 75 mm for females); central gular scales much enlarged, surrounding scales diminishing in size gradually toward the periphery of the gular region; frontal and frontoparietal scales entire; three parietal scales; total number of femoral pores moderate; number of dorsal granules around the body (GAB) and occiput to rump (GOR) low; no preanal spurs; broad middorsal stripe bordered laterally by a fine white stripe; black dorsolateral stripe bordered ventrally by a fine white stripe; no narrow, light-colored vertebral stripe.

Range. Known only from the type locality and from Honda, Departamento Tolima, Colombia.

Remarks. Dunn (1943) diagnosed *Ameiva festiva niceforoi* (=*A. niceforoi*) as "A form of *festiva,* identical with it in size, proportions, and in scalation, but remarkably different in markings." In addition to color pattern (Fig. 1A), *niceforoi* differs from *festiva* in a number of characters of scutellation. In color pattern, *niceforoi* is virtually identical to female or subadult male *A. leptophrys* but differs from *leptophrys* in numerous scale characters. Some pertinent differences among the three species are summarized in Table 1. Because geographic variation is marked (Echternacht, 1970), means of characters of scutellation for an entire species tend to mask similarities between *niceforoi* and samples of other species drawn from nearby localities. For this reason, means for nearby samples are given as well as those for the entire species. In addition to the total number of femoral pores, GAB and GOR, *niceforoi* differs from *leptophrys* in the arrangement of scales peripheral to the enlarged central gulars. In *leptophrys* the posterior gular scales are much reduced in size

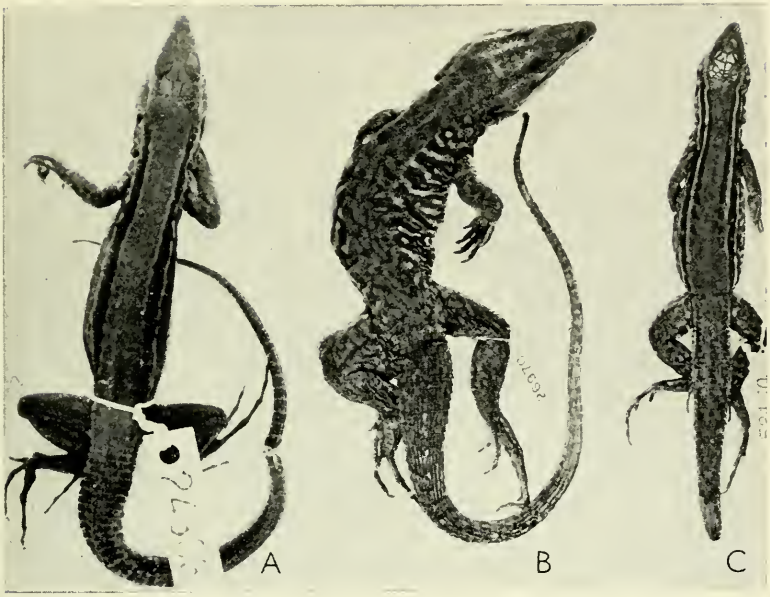

FIGURE 1. (A) *Ameiva niceforoi,* paratype (ANSP 24303: Sasaima, Depto. Cundinamarca, Colombia), snout-vent length 77 mm. (B) *Ameiva undulata miadis,* holotype (MCZ 26970: Isla del Maiz Grande, Depto. Zelaya, Nicaragua), 126 mm. (C) *Ameiva chaitzami,* paratype (MCZ 52170 [formerly UMMZ 90642]: Along Cahabón-Languín trail ca. 2 km N Finca Canihor, Depto. Alta Verapaz, Guatemala), 69 mm. All males.

relative to the anterior gulars. *Ameiva niceforoi* and *festiva* are similar in this respect.

No other South American species of *Ameiva* seems to be closely related to any of the three species discussed above. An *Ameiva* similar to *niceforoi* could have given rise to either *leptophrys* or *festiva* or to both, but the present chaotic situation with respect to the taxonomy of *Ameiva* in South America (Medem, 1969) precludes decisive conclusions concerning phylogenetic relationships. Studies in progress are designed to clarify this situation.

Other than the type series (ANSP 22784, 24300–303), only three specimens of *Ameiva niceforoi* are known: USNM 93500–93501 (Topotypes) and AMNH 35300 from Honda, Depto. Tolima, Colombia.

	niceforoi	*leptophrys*		*festiva*		
	Entire Sample	Entire Sample	Eastern Panamá	Entire Sample	Río Uré and Vic., Depto. Córdoba, Colombia	Condoto-Andagoya-Tado Area, Intendencia de Chocó, Colombia
Femoral Pores Males	31.0 29-34 4	49.1 42-61 112	48.5 44-52 12	40.8 33-55 273	42.5 38-47 21	39.2 37-42 9
Femoral Pores Females	29.8 28-31 4	44.7 34-53 100	45.4 41-52 9	40.0 32-50 260	41.5 37-48 11	39.8 36-43 8
GAB Males	127.0 113-141 3	153.8 127-182 201	151.0 140-162 21	182.5 145-221 244	187.0 172-202 19	192.8 181-205 8
GAB Females	122.5 120-125 2			179.8 143-213 233	177.8 162-188 10	196.6 175-213 8
GOR Males	217.2 201-235 4	235.5 182-285 209	233.9 212-301 23	261.1 209-324 273	271.4 248-307 19	249.2 236-269 9
GOR Females	215.0 209-221 4			259.5 215-312 264	261.9 215-290 12	251.0 233-282 8
Maximum Observed SVL Males	82	133	118	114	107	95
Maximum Observed SVL Females	75	129	113	129	99	95

Table 1. Comparison of *Ameiva niceforoi* with *A. leptophrys* and *A. festiva*. Upper number, sample mean; Middle numbers, range; Lower number, sample size. *Ameiva leptophrys* is not sexually dimorphic for GAB or GOR.

Ameiva undulata miadis Barbour and Loveridge

Ameiva festiva miadis Barbour and Loveridge, Bull. Mus. Comp. Zool., 69: 141-142, 1929 (Holotype: MCZ 26970. Type Locality: "Great Corn Island" [=Isla del Maiz Grande], Depto. Zelaya, Nicaragua. Collector: James L. Peters).

Ameiva undulata miadis, Dunn, Proc. Acad. Nat. Sci. Philadelphia, 92: 115, 1940. Villa, Rev. Biol. Trop., 15: 119, 1968.

Diagnosis. Ameiva undulata miadis (Fig. 1B) can be distinguished from *A. festiva* and other subspecies of *A. undulata* on the basis of its unique color pattern: No narrow, light-colored vertebral stripe; lateral pattern of blue (males) or gray-brown (females) bars on a black background extending from middorsal stripe to enlarged ventral scutes; broad middorsal stripe from occiput onto tail, much disrupted by transverse black blotches that are often continuous with the black background color of the flanks; sexual dimorphism in color, but not pattern, in adults.

Range. Known only from Islas del Maiz, Depto. Zelaya, Nicaragua.

Remarks. With the exceptions noted above, *Ameiva undulata miadis* is similar to other subspecies of *undulata* that have barred flanks (see Echternacht, 1970). Dunn (1940) and Villa (1968) have briefly alluded to the relationship of *miadis* with *undulata*

Barbour and Loveridge (1929) considered *Ameiva festiva miadis* (=*A. undulata miadis*) to be intermediate between *A. festiva* and *A. ruthveni* (=*A. leptophrys*). Color pattern alone distinguishes *miadis* from *leptophrys,* but in addition, the peripheral gular scales of *undulata* are like those described for *niceforoi* above and differ from those of *leptophrys* in the same manner. Also, in *leptophrys* the postnasals are not in contact with the prefrontal scales, whereas in *undulata* these scales are in contact.

The nearest known mainland populations of *Ameiva festiva* are at Bluefields, Depto. Zelaya, Nicaragua, about 85 kilometers west of Isla del Maiz Grande. *Ameiva festiva* from Bluefields are typical of the species in having a well-defined vertebral stripe in all but large adults and in having little barring on the flanks. Nearest known populations of *leptophrys* are in the southeastern lowlands of Costa Rica, and the nearest populations of *undulata* are in northeastern Honduras, western Nicaragua, and northwestern Costa Rica. Four specimens of *undulata* (ANSP 15438–15441) from Huaunta Haulover, Depto. Zelaya, Nicaragua, about

150 kilometers north-northwest of Isla del Maiz Grande, may indicate an isolated population there. In color pattern, the *undulata* from Islas del Maiz most closely resemble those from near Catacamas, Depto. Olancho, Honduras. In these Honduranian *Ameiva,* the middorsal stripe is heavily blotched, but the blotches are never continuous onto the flanks.

Island populations of Middle American *Ameiva* (with the exception of *quadrilineata*) tend to have a relatively high GAB count when compared to mainland samples of the same species (see Echternacht, 1970). Although the mean for this character does not differ statistically from those of certain mainland samples examined, it is the highest recorded for the species (*A. undulata*: $\bar{x} = 149.5$, standard deviation of the mean = 16.5, range = 108–202, N = 918. *A. u. miadis:* $\bar{x} = 186.3 \pm 9.3$, range = 165–202, N = 42).

Nothing has been reported of the ecology of *Ameiva undulata miadis.* I was able to make some observations on June 4-8, 1966. The lizard is very common on Isla del Maiz Grande and I found it particularly abundant in clearings within the coconut groves that cover the island (Fig. 2). It was also common in the shrub and

FIGURE 2. Habitat of *Ameiva undulata miadis* on Isla del Maiz Grande, Depto. Zelaya, Nicaragua. June 1966.

grassy vegetation along the airstrip and in clearings around buildings. None were seen on open beaches. Individuals often were encountered basking or foraging on or around fallen palm fronds. Activity extended from dawn until dusk, but more lizards were seen early in the day than in late afternoon. The lizards were not active in rain. Hatchlings with clearly delineated umbilical scars were observed. The chin, gular region, and anteriormost part of the chest of many males was bright reddish orange. In others, this area was pale blue. Such dichromatism is widespread among species of *Ameiva* and may be associated with reproductive condition. Evidence is lacking on this point. English-speaking residents of the island refer to the *Ameiva* simply as "lizard," although they have specific names for *Iguana iguana* and *Ctenosaura similis,* both of which are common.

Ameiva chaitzami Stuart

Ameiva chaitzami Stuart, Proc. Biol. Soc. Washington, 55: 143, 1942 (Holotype: UMMZ 90638. Type Locality: "Along Cahabón-Languín trail about 2 km north of Finca Canihor . . . , Alta Verapaz, Guatemala." Collector: L. C. Stuart).

Ameiva undulata thomasi Smith and Laufe, Univ. Kansas Sci. Bull., 31: 47-50, pl. IA, 1946 (Holotype: FMNH 100006. Type Locality: "La Libertad, Chiapas, near Río Cuilco where it crosses the Guatemalan border," México. Collector: Henry D. Thomas). New synonymy.

Diagnosis. Ameiva chaitzami (Fig. 1C) can be distinguished from its congeners by the following combination of characters: Small size (maximum observed SVL 85 mm for males, 75 mm for females); central gular scales enlarged, in longitudinal series; gradual reduction in size of scales radiating outward from the central gulars; prefrontals in contact with postnasals; three parietal scales (four if median parietal divided); transverse row of abruptly enlarged mesoptychial scales; usually eight transverse rows of ventral scutes at midbody; moderately narrow middorsal stripe (mean width in terms of granules 37.1, N = 61); no narrow, well-defined vertebral stripe; often a dark secondary stripe medial to the dorsolateral light stripes; dorsolateral blotches of adult males fused to the dorsolateral light stripe so that the latter has a well-defined dorsal border, an irregular ventral border. The latter character alone will distinguish *chaitzami* from *undulata* with certainty.

Range. Valleys of the upper tributaries of the Río Grijalva in Chiapas, México, and west-central Guatemala, from the vicinity of Finca Canihor, Depto. Alta Verapaz, Guatemala, and near Poptún, Depto. El Petén, Guatemala.

Remarks. Stuart (1942) diagnosed *Ameiva chaitzami* as "An *Ameiva* almost identical with *Ameiva undulata stuarti* Smith from which it may readily be distinguished by the fact that the median parietal is divided longitudinally to produce four instead of three parietals." The posterior scales on the dorsal surface of the head is an unstable character among Middle American species of *Ameiva,* and diagnoses based on scales in the area are unreliable (Echternacht, 1970). Considering *undulata* only, I noted the median parietal to be divided or semidivided in 22.4 per cent of 1043 specimens obtained from throughout the range of the species. This is probably a conservative estimate of the frequency of occurrence of this condition, because the information was not noted early in the study. There seem to be no geographic trends associated with the condition of the median parietal. At least 38 of 45 samples contained individuals with divided or semidivided median parietals. Samples having a high frequency of occurrence of division were as follows: near Chinandega, Depto. Chinandega, Nicaragua (55 per cent, N = 31); Piedras Negras, Depto. El Petén, Guatemala (72 per cent, N = 32); Canihor, Depto. Alta Verapaz, Guatemala (50 per cent, N = 30); near Panajachel, Depto. Sololá, Guatemala (48 per cent, N = 29); Sabana de San Quintín, Chiapas, México (100 per cent, N = 10); near Las Tazas and Florida, Chiapas, México (90 per cent, N = 30). Three samples of *chaitzami* yielded the following frequencies: Comitán, Chiapas, México, 3 per cent (N = 30); near San Antonio Huista, Depto. Huehuetenango, Guatemala, 10 per cent (N = 31); near Finca Canihor, Depto. Alta Verapaz, Guatemala, and near Poptún, Depto. El Petén, Guatemala, 89 per cent (N = 9). Six of the nine in the last sample constitute the type series. At the type locality and at Poptún, *chaitzami* is sympatric with *A. undulata hartwegi* Smith, a large subspecies quite distinct in color pattern and scutellation from *chaitzami.* The samples from Canihor and Piedras Negras, Guatemala, and from Sabana de San Quintín, Chiapas, are *hartwegi.* Elsewhere within its range, samples of *hartwegi* have from 13 to 30 per cent of individuals with divided or semidivided median parietals. It is noteworthy that the holotype of *hartwegi* (FMNH 108600), obtained across the Río Usumacinta from Piedras Negras, has a divided median parietal.

Smith and Laufe (1946) discussed the evolution of *Ameiva undulata* and recognized several new subspecies, but they apparently did not examine specimens of *chaitzami*. The description of *A. u. thomasi* (Smith and Laufe, 1946) agrees with that of Stuart (1942) for *chaitzami* in most respects. I have examined the type specimens of both and consider them to be conspecific. The samples cited above from Comitán and near San Antonio Huista are from within the range of *thomasi* as described by Smith and Laufe (1946).

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GENERIC RELATIONS AND SPECIATION PATTERNS IN THE CARACARAS (AVES: FALCONIDAE)

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ABSTRACT. The caracaras are a group of American Falconidae occurring from temperate and subtropical North America southward to extreme southern South America and the Falkland Islands. The taxa of caracaras appear to be closely interrelated. It is suggested that they be classified in two genera: *Daptrius* (forest caracaras; two sympatric species), and *Polyborus* (nonforest caracaras; two species-groups: the *chimachima* and *plancus* species-groups, with two and three species, respectively). Former classification advocated the use of four genera. Speciation is long completed in *Daptrius* and in the *Polyborus chimachima* species-group. In the *Polyborus plancus* species-group, however, several phenomena are evidence of active species formation. Geographical isolates exist that are morphologically differentiated enough to be considered borderline cases between species and subspecies. Some of the cases of geographical isolation in the caracaras can be related to climatic and vegetational changes following glacial events of the Pleistocene.

INTRODUCTION

This paper constitutes the fourth of a series stemming from studies on speciation in Andean birds (see Vuilleumier, 1968, 1969, 1970).

I shall discuss, first, the generic classification of the caracaras, and secondly, the patterns of distribution, geographical variation and speciation in these birds, with particular emphasis on the Andean taxa. I shall deal either with problems not, or only little, covered by Brown and Amadon (1968) in their recent book, or

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with controversial issues, especially when my own conclusions differ from theirs.

The data were obtained from examination of about 250 skins and some skeletons; and from field studies on the habitat preferences, general behavior, and distribution of five taxa of caracaras made over a period totaling thirteen months during trips to South America in 1964, 1965, and 1967-68.

THE CARACARAS

The 7 to 10 or 11 species of caracaras can be distinguished from other Falconidae more by their vulture-like external morphological characters and associated scavenging habits, than by clear-cut anatomical characters (Friedmann, 1950: 719). They differ from true falcons, however, in their habit of building their own nest, as pointed out by Brown and Amadon (1968: 23, 104). The problem of whether the caracaras should be accorded taxonomic rank within the Falconidae, and if so, which one (e.g., subfamily, tribe), will not be discussed here.

The species of caracaras have traditionally been placed in four genera (see, e.g., Peters, 1931; Hellmayr and Conover, 1949; Friedmann, 1950; de Schauensee, 1966; Brown and Amadon, 1968): *Daptrius* Vieillot, 1816, with two species; *Milvago* Spix, 1824, with two species; *Phalcoboenus* d'Orbigny, 1834, with two to four species; and *Polyborus* Vieillot, 1816, with one to three species. (The long controversy over the names *Polyborus* versus *Caracara* Merrem, 1826, was resolved by Amadon (1954), who showed that "Vieillot's diagnosis of *Polyborus* applies to the Caracaras," so that "the diagnosis sustains the name." *Caracara* must, therefore, go into synonymy, and the issue can be considered closed.)

As a group, the caracaras are distributed from temperate North America southward to Central and South America, ranging as far south as the Falklands and the islands off Tierra del Fuego. Several species have very broad ranges, especially *Polyborus plancus,* the distribution of which encompasses almost that of the entire group. Other species are, on the contrary, quite localized geographically. For example, the extinct *Polyborus lutosus* occurred only on Guadalupe Island off Baja California, and the living *Phalcoboenus australis* breeds on a handful of small islands off the southern coast of Tierra del Fuego and on the Falklands.

Correlated with the broad distribution of the caracaras is their ecological diversity. As a group, these birds inhabit most vegetation formations found in their geographical range, from desert scrub to tropical lowland wet forest, and including the highest zones of Andean vegetation. About the only major type of vegetation not favored by caracaras is montane tropical wet forest (or cloud forest).

All the taxa of caracaras are scavengers, but should perhaps be viewed as omnivorous, since their diet also includes live prey (vertebrates and invertebrates) and vegetal matter (see, e.g., Hudson, 1920: 62-88; Wetmore, 1926: 92-96; Haverschmidt, 1962: 157-158; Friedmann, 1927: 157; Friedmann and Smith, 1950: 450-451, and 1955: 486-487; Brown and Amadon, 1968). Among the most notable food specializations of the caracaras is the habit of *Polyborus plancus* of attacking domestic animals the size of sheep (Johnson, 1965: 263), and the marked predilection shown by *Daptrius americanus* for colonial wasps (Skutch, 1959).

Most caracaras are social, at least during the nonbreeding season, and form intraspecific flocks that appear to be feeding associations. The larger-sized species may form smaller flocks than the smaller ones. Thus the largest flock of the osprey-sized *Polyborus plancus* I have observed comprised about 15 birds, while I have often seen much larger flocks of the kestrel-sized *Milvago chimango*. The intraspecific gregariousness of some of the smaller species may also extend to the breeding season. Drury (personal communication) observed a colony of *Milvago chimango* where the nests were only about 30 feet (ten meters) apart. The caracaras also form associations with vertebrates other than birds. In Patagonia, *Milvago chimango* flocks are frequent near cattle and horses; I even saw one bird sitting on the flank of a lying horse, pecking from time to time at the skin, perhaps to eat ticks. Hudson (1920: 70) mentioned that *M. chimango* "follows the plough," thus playing the part of gulls (*Larus*) elsewhere. The habit of following moving vehicles from which scraps of food can be collected has been observed in *Phalcoboenus megalopterus* along the Yungas Road in La Paz, Bolivia (Niethammer, 1953: 265; personal observation), and in *Polyborus plancus* along a railroad in the Bolivian Chaco (Eisentraut, 1935: 391). The gregarious behavior exhibited by the caracaras may be correlated to a large extent with their scavenging habits, yet, from my own observations, I would judge their behavior to be much more plastic and diverse than that of

other scavengers such as Old World or New World vultures (Cathartidae and Aegypiinae, respectively).

ANALYSIS OF SOME CHARACTERS OF THE CARACARAS

Size

The caracaras vary considerably in size, as several authors (Friedmann, 1950; Brown and Amadon, 1968) have already pointed out. This variation is obvious if wing length, in the absence of data on weights, is used as an indicator of overall body size (Table 1). Taxonomists have often been bothered by size differences between species, and have been reluctant to place in the same genus closely related species which differed conspicuously in size but in few, or no. other characters. This attitude might have been prevalent among the ornithologists who worked with caracaras, because the two smallest species belong in the genus *Milvago* and the largest species in *Phalcoboenus* and *Polyborus*. Yet the two species of *Daptrius* bridge the gap between these extremes. I therefore believe that size should not be given undue weight in the supraspecific classification of the caracaras. In other Falconidae, notably in the genus *Falco,* similarly large size differences between species have not prevented their inclusion in the same genus.

Proportions

In a number of bird taxa, a proportionately short tarsus is correlated with arboreal habits, and a long tarsus with more terrestrial habits. Most species of caracaras are both arboreal and terrestrial, but some definite trends toward one or the other of these habits exist, especially in regard to feeding habits. Thus *Polyborus* and *Milvago* are often seen perched on trees, and they breed in trees, but they do a lot, perhaps most, of their foraging for food on the ground. The species of *Phalcoboenus* (with the possible exception of *P. albogularis*) seem to forage entirely on the ground, and breed in cliffs and rocky slopes; they do on occasion perch on buildings. The species of *Daptrius* seem at variance with the other three genera because they do some, perhaps even a substantial, portion of their foraging for food in trees.

From this summary one would thus expect the species of *Daptrius,* which are more arboreal than the other caracaras, to have proportionately shorter tarsi than other species. Figure 1 shows a

TABLE 1

Variation of some characters among the caracaras

Taxon	*Wing length (mm)*	*Adult color*	*Immature color like adult*	*Facial skin naked (color)*	*Nostril shape*	*Habitat*
ater	294-317 (304.6) (N = 8)	black & white	no (brownish)	yes (yellow-red)	rounded	forest
americanus	327-406 (362.5) (N = 36)	black & white	yes	yes (vermilion)	rounded	forest
chimachima	255-305 (282.9) (N = 40)	brown & whitish	no (brownish)	yes (yellowish)	rounded	open woodland
chimango	276-305 (290.0) (N = 11)	brown	yes	no	rounded	open woodland
plancus	356-451 (394.6) (N = 66)	brown & white	no (brownish)	yes (yellow-red)	bean-shaped	open scrub to woodland
lutosus	402-421 (411.5) (N = 2)	dark brown	yes	yes (yellow)	bean-shaped	open country
australis	406-424 (411.8) (N = 5)	dark brownish black with white and cinnamon	no (dark brown)	yes (orange-yellow)	rounded	steppe
caruncula tus	370-388 (378.7) (N = 3)	black & white	no (brownish)	yes (orange-red)	rounded	montane steppe
megalopterus	358-403 (382.5) (N = 17)	black & white	no (brownish)	yes (orange-red)	rounded	montane steppe
albogularis	357-392 (371.8) (N = 6)	black & white	no (brownish)	yes (yellow-orange)	rounded	forest (?)

scatter diagram of tarsus length plotted against wing length (representing body size in the absence of weight data) in the caracaras. The two species of *Milvago,* although overlapping considerably in wing length, show little overlap in tarsus length. The southern species, *M. chimango,* is decidedly longer-legged than the northern one, *M. chimachima.* This difference, especially in regard to the zone of sympatry of the two species, is discussed again below in the section on speciation in these birds. *Daptrius ater* has somewhat longer wings than either species of *Milvago,* but its tarsal measurements overlap fully with those of *M. chimachima.* Yet *D. ater* would seem more arboreal than *M. chimachima.* The arboreal *Daptrius americanus* overlaps with the more terrestrial *Phalcoboenus megalopterus, P. albogularis,* and *Polyborus plancus* in wing length, but has a much smaller tarsus. In this case the difference in tarsus size appears to correspond to a difference in habits.

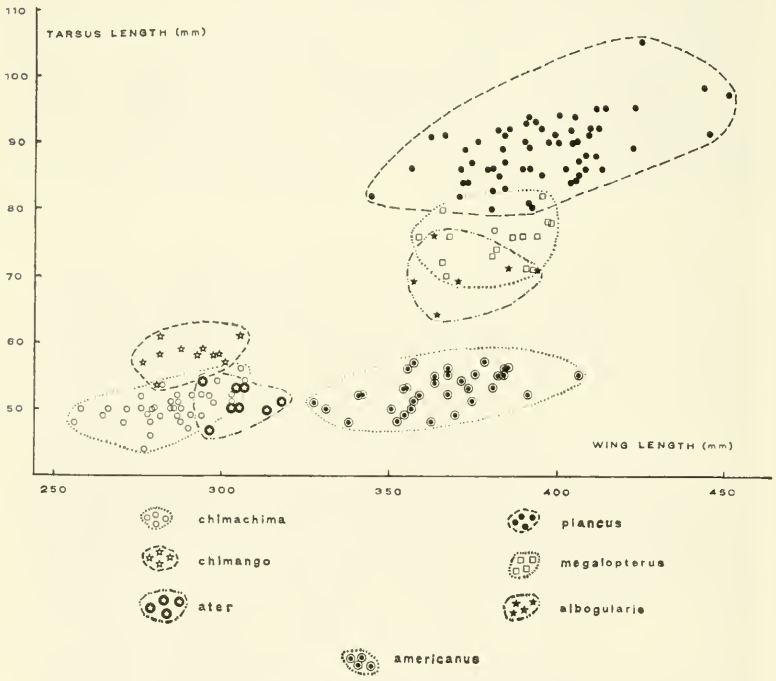

Figure 1. Tarsus length plotted against wing length in seven taxa of caracaras.

It is worthy of note that the species of *Phalcoboenus* closest to *D. americanus* in tarsus length is *P. albogularis* (see Fig. 1) said by Olrog (1948: 478; 1950: 520) to occur in forests and thus to diverge from the habitat preferred by *P. megalopterus*.

On the basis of the proportions of tarsus and wing lengths plotted on Figure 1, *Milvago chimango, M. chimachima,* and *Daptrius ater* would form one group of species closely similar to each other, overlapping greatly in both wing and tarsus length. A second such group would include *Phalcoboenus* and *Polyborus,* while *Daptrius americanus* appears clearly distinct from all other species, yet intermediate between the two groups.

Interspecific variation in tail length is summarized in Table 2. When handling skins, *Daptrius americanus* appears distinctly longer tailed than the other species of caracaras. If the tail/wing ratios, instead of the absolute tail lengths, are compared among the species of caracaras, then a smooth variation is detected, from the proportionately short-tailed *Polyborus plancus* and *Phalcoboenus megalopterus* to the long-tailed *Milvago chimachima* and *Daptrius americanus*. No groups of caracaras can be established on the basis of relative tail length.

TABLE 2

Variation in tail length, expressed in percent of wing length, among the caracaras. The taxa are ranked in order of increasing tail/wing ratio. Both sexes, and adult and subadult birds included.

Taxon	*Tail/Wing × 100*		*Sample Size*
	Range	*Mean*	
plancus	50.8-58.1	53.9	42
megalopterus	53.1-57.4	55.5	13
carunculatus	—	55.6	1
chimango	54.8-58.7	57.3	5
albogularis	54.1-64.7	58.4	5
australis	57.5-61.5	59.4	4
ater	58.4-63.5	61.1	6
lutosus	—	62.7	1
chimachima	60.9-70.2	66.2	25
americanus	62.2-74.6	68.4	36

Plumage Color and Pattern

Good descriptions of both adult and immature plumages of caracaras have been given by Friedmann (1950) and Brown and Amadon (1968), who should be consulted for full details. The main colors of adult and immature plumages are summarized in Table 1.

Adult caracaras vary from a brown, rather unpatterned plumage (such as is found in a variety of birds of prey) to a highly patterned plumage. Thus *Milvago chimango* has a brown plumage, variegated somewhat with barrings, reminiscent of the plumage of some kites of the genus *Milvus*. The plumages of both species of *Daptrius*, and of the three Andean species of *Phalcoboenus* (*carunculatus, megalopterus,* and *albogularis*) are very different from those of the other caracaras. These birds are strikingly marked with black and white patterns, and remind one of gallinaceous birds such as *Crax*.

Immature caracaras are less varied in their plumages. Most of them are brownish with patterns of barring or streaking, with the exception of the immature *Daptrius americanus,* which is like the adult. The dimorphism between immature and adult can be very well marked, as in *Phalcoboenus carunculatus, P. megalopterus,* and *P. albogularis;* or poorly marked, as in *Daptrius americanus* or *Milvago chimango;* or intermediate, as in *Polyborus plancus* and *P. lutosus*.

In spite of the variation in plumage color and pattern exhibited by the different species of caracaras, certain basic resemblances are evident in the group as a whole when adult and immature plumages are compared together. For example, the immatures of *Milvago chimachima, Phalcoboenus carunculatus, P. megalopterus, P. albogularis, Polyborus lutosus* and *P. plancus* are all very similar to one another, as they are to the adult of *Milvago chimango*. Thus, regardless of the intraspecific variability between immatures and adults on the one hand, and the interspecific variability among adults on the other, *Milvago, Phalcoboenus,* and *Polyborus* all appear to have similarities in plumage color and pattern.

In every genus except *Polyborus,* there is a dichotomy between one or more species that have different immature and adult plumages, and one or more species that have quite similar immature and adult plumages. This dichotomy is obvious in *Milvago,* with

chimango plumages much alike, and *chimachima* unlike; in *Phalcoboenus,* with *australis* plumages much alike, and with *carunculatus-megalopterus-albogularis* plumages very different. The dichotomy is still present, but much less obvious, in *Daptrius,* with *americanus* plumages alike and *ater* plumages slightly different. Correlation between this dichotomy and patterns of geographical distribution among closely related species is not readily apparent. In *Milvago* and *Phalcoboenus,* the species which differ least in their adult and immature plumages are the two southern ones; but in *Milvago* alone, there is an important geographical overlap between *chimango* and *chimachima,* whereas there is no or only a very narrow overlap between the southern *australis* and the more northern *carunculatus-megalopterus-albogularis* complex. In *Daptrius* (dichotomy poorly marked), there is almost complete overlap between the ranges of the two species, since the range of *ater* is almost entirely contained within that of *americanus.* In *Polyborus* (no, or almost no dichotomy), *lutosus* and *plancus* are entirely allopatric. (The possible ecological significance of the immature and adult dimorphism is discussed below under habitat preferences.)

If one were to consider the immature-like plumage of some sexually mature birds as being a primitive condition, and the strikingly different plumage in other mature birds as an advanced one (i.e., secondarily developed during the evolutionary history of the caracaras), then *Polyborus* and *Daptrius* might be thought to be more primitive than the other two genera. If a brownish, barred and streaked immature plumage were considered a more primitive condition, then *Daptrius* is more advanced in this character than the three other genera, because in that genus, immatures are hardly different from adults, being also conspicuously patterned in black and white.

Naked Facial Skin

Every species in the genera *Polyborus, Phalcoboenus,* and *Daptrius* has brightly colored naked skin between the bill and the eye, and often around the eye or even the throat. In the genus *Milvago,* only *M. chimachima* has naked facial skin; *M. chimango* has a fully feathered head. The area of unfeathered skin varies from species to species among those that have naked facial skin. In the species of *Phalcoboenus,* this variation is geographical. In *Phalcoboenus carunculatus* (Colombia and Ecuador), the surface of facial skin is extensive, and the throat is even adorned by fleshy wattles. In

P. megalopterus (Peru, Bolivia, and northern Chile-Argentina), only the lores are unfeathered, while the throat is largely feathered. In *P. albogularis* (Patagonia), the extent of bare loral skin is smaller than in *megalopterus*. Finally, in *P. australis* (southernmost islands of South America), the facial skin is almost entirely feathered, but there are wattles on the breast instead. The difference between *P. australis* and *P. carunculatus-megalopterus-albogularis* may be related to the fact that *australis* is sympatric with *Polyborus plancus,* a species having extensive naked facial skin, whereas the other three species of *Phalcoboenus* are the only caracaras in their respective ranges.

The naked facial skin in the caracaras varies from salmon pink to rose-red and from yellowish to bright red (see Table 1). This variation is both intra- and interspecific. I have seen the facial skin of one individual of *Polyborus plancus* change, in a few seconds, from pale yellow to salmon-pink and finally to vivid red. Such a rapid change cannot easily be ascribed to hormonal influences, but is more likely to be due to a sudden flush of blood to the superficial vessels of the skin. Brown and Amadon (1968: 738) mention a reverse change in *P. plancus*: "bare facial skin carmine red, changing to yellow when excited."

The variation in facial skin color in the caracaras (Table 1) seems too extensive within species, and too restricted between species (differences between, say, yellow and orange, or orange and red seem relatively slight) to be important as a species-specific means of recognition. Presence or absence, together with color and area of unfeathered skin might, however, play such a role among true sympatric species, e.g., *Phalcoboenus australis* and *Polyborus plancus* already cited, or *Milvago chimango* and *M. chimachima.*

Nostril Shape

I have examined skulls of *Polyborus plancus* (several specimens), *Phalcoboenus australis* (4), *Daptrius* sp. (1), and *Milvago* sp. (3). *Polyborus plancus* has slanted, elongated nostrils (bean-shaped), while *Phalcoboenus australis, Daptrius* sp., and *Milvago* sp. all have rounded nostrils. This difference is also visible on the cere of study skins and seems to be confined to *Polyborus* (Table 1), since only *P. lutosus* and *P. plancus* have bean-shaped nostrils. Swann (1925: 66) and Friedmann (1950: 545-546) used this

difference in nostril shape, together with other characters, as diagnostic features to key out the genera of caracaras. I do not know what the biological significance of this difference may be.

Habitat Preferences

The preferred habitats of *Milvago, Phalcoboenus,* and *Polyborus* include a variety of nonforest types: open scrub, grassy pampas, tussock-grassland, pastures, treeless cultivated farmland, open thorny chaco, savanna woodland, and open plantations. *Phalcoboenus albogularis* may be an exception, since Olrog (1948: 478; 1950: 520) reports it as a forest bird.

Both species of *Daptrius* are inhabitants of tropical forest and contrast markedly with the other caracaras in this feature. The distribution of *ater* and *americanus* corresponds to the distribution of wet lowland rain forest in Central and South America, but the actual preference of these species seems to be less for the forest interior than for more open situations within or along the forest: river banks, small clearings, secondary growth, mangroves, and tree-tops. The plumage pattern of both species of *Daptrius,* especially *D. americanus,* is most similar to that of adults of *Phalcoboenus carunculatus* and *P. megalopterus,* which inhabit high Andean steppes, an environment that differs in every respect from that of *Daptrius.* This basic morphological similarity among taxa of widely distinct ecological preferences seems to be more easily understandable on an hypothesis of close relationship than on one of convergent evolution. The fact that the species of *Phalcoboenus* mentioned above have a very different immature plumage, while those of *Daptrius* are far less dimorphic between adult and immature, might be a correlate of environmental differences between the two genera. In the open habitats of the high Andes there is never more than one species of caracara at any one locality (diversity = 1). Because congeneric competitors are absent, the sharp dimorphism between adults and immatures of *Phalcoboenus* may consequently reflect the results of slightly relaxed selective pressures. In the tropical lowland forests, however, there are two sympatric species of caracaras (diversity = 2), so that selection through interspecific competition might possibly limit the range of intraspecific variability, thus resulting in the evolution of similarity (monomorphism) between immatures and adults of *Daptrius.* The difference in size (character divergence) between the two species

of *Daptrius,* which are sympatric, may be relevant here. Being so different from each other (no overlap in range of wing lengths), they should compete very little for food (see Schoener, 1965). The interspecific difference in size, together with the lack of dimorphism between age categories in *Daptrius,* may be roughly equivalent ecologically to the striking dimorphism within high Andean *Phalcoboenus,* which do not have any sympatric congeners. In *Milvago,* where the two species are largely allopatric, one observes a considerable overlap in wing lengths between the two, but one of the species is conspicuously dimorphic (*chimachima*), whereas the other is not. Therefore, the situation in *Milvago* appears intermediate to that in both *Daptrius* and *Phalcoboenus.* I believe this intermediacy is also found in the habitats occupied by *Milvago* (such as open woodland, savannas) that are more or less intermediate between lowland wet forest (occupied by *Daptrius*) and barren high Andean steppes (occupied by *Phalcoboenus*).

Summary of Character Analysis

If the characters discussed above are examined separately, the variation among some of them shows the following possible grouping within the caracaras. (a) *Polyborus* is distinct in nostril shape from the other genera. (b) *Daptrius* and *Phalcoboenus* are closer to each other than to other genera since both have a strikingly patterned black and white adult plumage. (c) The immature plumages of *Milvago, Phalcoboenus* and *Polyborus* appear extremely similar to one another, and differ, as a group, from those of *Daptrius.* If both adult and immature plumages are used, together with habitat preferences, the two species of *Daptrius* appear to stand out against most other species. First, the immature plumage of *Daptrius,* when distinct from that of the adult (as in *D. ater*), is quite different from the brownish, streaked or barred immature plumage of all other species except *Phalcoboenus australis.* Secondly, the forest habitat of the species of *Daptrius* differs from the nonforest habitats of the species in the other genera, with the possible exception of *Phalcoboenus albogularis.* (The remaining characters [naked facial skin and size] seem of little or no use in establishing groups within the caracaras.)

I can only conclude from this analysis that all caracaras appear to be closely interrelated, but that *Daptrius* is less similar to the other three genera than these are to each other.

CLASSIFICATION

The splitting of the caracaras into four genera, endorsed by most taxonomists, does not seem to reflect properly the close relationships of these birds. Since the lumping of all caracaras into a single genus may be going somewhat too far in the opposite direction, I suggest here a third possibility, which is to put the caracaras inhabiting nonforest habitats in a single genus (*Polyborus,* including *Milvago* and *Phalcoboenus*) and to keep the forest caracaras in a second genus (*Daptrius*). Further subdivisions within the nonforest caracaras can be made by using species-groups and superspecies, which do not burden the nomenclature with additional names (as pointed out by Cain, 1954), yet permit a finer hierarchy between the genus and species levels.

I present below a classification outline of the caracaras, including species-groups and superspecies. Each species-group represents a former genus. The grouping of some species in a superspecies (included in braces) is given here in anticipation of the discussion on speciation in the next section of this paper. The sequence of taxa in this list is arbitrary, and does not pretend to suggest that some taxa are more primitive than others, since such decisions would be guess work.

Genus *Daptrius* Vieillot, 1816 (forest caracaras)

D. ater Vieillot, 1816

D. americanus (Boddaert, 1783)

Genus *Polyborus* Vieillot, 1816 (nonforest caracaras)

1. *chimachima* species-group

   P. chimachima Vieillot, 1816

   P. chimango Vieillot, 1816

2. *plancus* species-group

   P. plancus (Miller, 1777) (includes *lutosus* Ridgway, 1876, considered by some authors as a separate species)

   australis superspecies

   { *P. australis* (Gmelin, 1788)
   { *P. megalopterus* (Meyen, 1834) (includes *carunculatus* (Des Murs, 1853), and *albogularis* Gould, 1837, considered by some authors as two separate species)

VARIATION AND SPECIATION IN *DAPTRIUS*

Of the two species of *Daptrius,* only *D. americanus* shows geographical variation. This variation seems to be a cline of diminishing size, as measured by wing length, from Guatemala southward through Central America to South America. According to Brown and Amadon (1968), the populations from "southern Brazil" may show an increase in wing length over those from farther north in South America. This increase is in fact quite sharp, and is illustrated by Figure 2. The disjunction may reflect absence of gene flow between birds from the Amazon Valley and those from the uplands of Brazil. The birds living in the coastal forests of southern Brazil and in the gallery forests of the Paraná-Paraguay drainage system of south-central Brazil may be ecologically isolated from birds living in forests of the Amazon Valley by parts of the central Brazilian plateau, which are covered by extensive open savannas and campos.

Any inferences that might be drawn about the possible evolutionary history of this genus are prevented by the considerable sympatry between *ater* and *americanus* (see map 76 in Brown and Amadon, 1968).

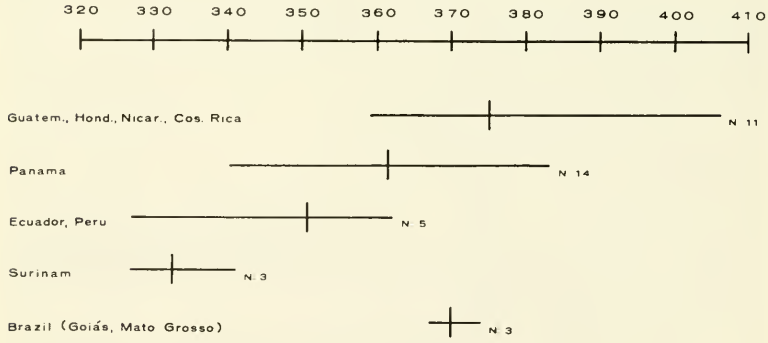

Figure 2. Geographical variation of wing length in *Daptrius americanus.* Measurements are in millimeters. Horizontal bars: range of measurements; vertical bars: means.

VARIATION AND SPECIATION IN *POLYBORUS*

1. The *chimachima* Species-Group

The two species of this group, which constitute the former genus *Milvago,* are largely allopatric. *Polyborus chimachima* occurs in southern Central America (Costa Rica and Panama) and in South America from Colombia and Venezuela in the north to northern Argentina in the south, and *P. chimango* from northern Argentina southward to southernmost South America. They are sympatric, however, over a relatively broad zone, including Rio Grande do Sul in southern Brazil, parts of northern Argentina, Uruguay, and Paraguay, and southern Bolivia westward to the foothills of the Andes.

Polyborus chimachima shows color and size variation. Tail and culmen length appear to vary clinally, and to increase from south to north, whereas the reverse seems to be true of wing length (see Fig. 3).

Polyborus chimango shows geographical variation that seems to conform to eco-geographical rules, since the southernmost birds are the largest (Bergmann's rule), and the birds occurring along the wet, forested Andean slopes are darker than those living in the drier, grassy and shrubby plains of central Argentina (Gloger's rule).

Geographical variation in *P. chimango* has been recognized taxonomically by the naming of three subspecies. Two of them, *temucoensis* (Andean slopes birds) and *chimango* (open plains birds) intergrade broadly. The third subspecies, *fuegiensis,* seems restricted to the island of Tierra del Fuego, but is probably merely the southward end of a north to south cline of increasing size. Interestingly, the southern populations, from Tierra del Fuego and the mainland of southern Patagonia, appear to leave their breeding grounds to migrate northward as far as northern Argentina (Olrog, 1962: 112-113) in the southern hemisphere winter.

Although *P. chimachima* and *P. chimango* are undoubtedly very close relatives, they have diverged morphologically rather considerably. One of the differences has been mentioned earlier: the immature plumage of *chimango* is very similar to that of the adults, whereas the immature *chimachima* is quite unlike the adult. Another difference between the two species may be ecological. As I

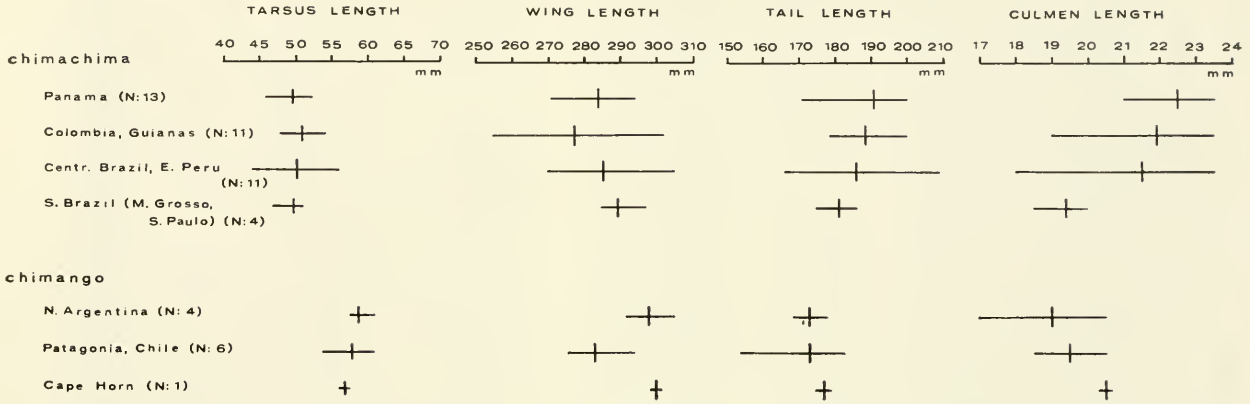

Figure 3. Geographical variations of tarsus, wing, tail, and culmen lengths in *Polyborus chimachima* and *P. chimango*. Horizontal bars: range of measurements; vertical bars: means.

judge from personal observations and literature records, *P. chimachima* may generally prefer somewhat denser, more wooded, habitats than *P. chimango,* but no study of a possible habitat segregation has been undertaken in the area of sympatry. If tarsus length reflects whether a bird is more or less arboreal, then variation between *P. chimachima* and *P. chimango* in this character is instructive. That *P. chimachima* populations have shorter tarsi than those of *P. chimango* (see Fig. 3) suggests that the latter may be less arboreal than the former. Whether this difference is true character divergence should be examined carefully.

Brown and Amadon (1968: 739) say that the two species "may be regarded as a super-species." Even if a broad superspecies concept is embraced, it seems to me that the zone of overlap, considered together with the morphological differentiation between *chimachima* and *chimango,* clearly suggests that these two taxa are past the species borderline, and that application of the superspecies concept to their case may no longer be correct. As far as I know, hybridization does not take place between the two species where they are sympatric; a field study of the pair in their overlap zone would nevertheless be rewarding.

It seems most likely that the pair of species *chimachima* and *chimango* has originated by a straightforward process of splitting of one ancestral population into two. Yet secondary sympatry is too extensive to permit more speculation about the original isolation.

2. The *plancus* Species-Group

This group consists of *P. plancus* and the *P. australis* superspecies. The birds of this group are medium to large, and have brownish immature plumage with dark streaking and/or barring. The *P. plancus* species-group includes both the former genera *Polyborus* and *Phalcoboenus.* Brown and Amadon (1968: 730) remarked that *"Phalcoboenus australis* is in all respects intermediate" between *Polyborus* and *Phalcoboenus,* yet they kept the two genera distinct.

P. plancus is essentially a lowland species, while the members of the *P. australis* superspecies occur mostly in the Andes, in some localities at high altitudes. Where *plancus* meets members of the *australis* superspecies, as on the Falkland Islands and on islands off Tierra del Fuego, the two may live in habitat co-occupancy, but their ecological relationships have not been studied. In any

event, sympatry in the *P. plancus* species-group is very limited and geographically peripheral.

Polyborus plancus

Polyborus plancus has a broad distribution from the southern United States and Mexico to Tierra del Fuego and the Falkland Islands and exhibits extensive geographical variation. The birds from Florida, isolated from the remainder of the mainland North American birds, are closer geographically and morphologically to the Cuban ones (both are included in the subspecies *audubonì*). The birds of the population living on the Tres Marías Islands off western Mexico (subspecies *pallidus*) are morphologically differentiated from the nearest mainland populations (for a discussion of the characters of *pallidus,* see Grant, 1965: 12-14). The continental population living from eastern Panama southward to northwestern Peru near the Upper Marañon and Amazon Rivers (subspecies *cheriway*) are well marked. There is intergradation between *cheriway* and southern South American birds (subspecies *plancus*) in Brazil (see Hellmayr and Conover, 1949: 283-284).

The extinct *Polyborus lutosus* lived on Guadalupe Island (see e.g., Abbott, 1933; Greenway, 1958). The adults looked very similar to *plancus,* but white was replaced by brown, and there was no black on the abdomen; the immature was brown and streaked. This insular population was certainly well marked; it is considered here as having been a strong subspecies of *plancus.* Brown and Amadon (1968: 736) maintained *lutosus* as a separate species.

The *australis* Superspecies

The four nominal species (the former genus *Phalcoboenus*) included in this superspecies are Andean and Patagonian in distribution (Fig. 4). One of the species, *australis,* occurs only on islands off southern South America. The three others, *carunculatus, megalopterus,* and *albogularis,* occur along the Andean cordillera, from Colombia to Tierra del Fuego.

Polyborus australis is larger than the three other species, but resembles them in several other respects. The pattern of breast and abdominal streaks in the adults is especially reminiscent of the geographically distant *carunculatus. P. australis* breeds on the Falklands, where, according to Cawkell and Hamilton (1961), its numbers have decreased in the recent past. It also breeds on several islands off Tierra del Fuego (Staten and Navarino), and on islands of the Cape Horn Archipelago (for example, Grevy, Bayly,

Figure 4. Geographical distribution of the *Polyborus australis* superspecies. A question mark represents the alleged occurrence of *albogularis* at Puente del Inca, Mendoza (see Hellmayr and Conover, 1949: 277-278). Labeled localities are identified in the text.

Freycinet, Hershel: Olrog: 1950: 520). Reynolds (1932) observed one *P. australis* on Woodcock Island in the Beagle Channel, and Olrog (1948: 478) saw it at Yendegaia, along the southern coast of Tierra del Fuego, where he also collected *P. megalopterus albogularis* (see Fig. 4). This observation (not mentioned by Brown and Amadon, 1968: 731) implies that *P. australis* and *P. megalopterus albogularis* are narrowly sympatric on the main island of Tierra del Fuego, but this suggestion needs careful checking in the field. *P. australis* is sympatric with *P. plancus* on some islands off Tierra del Fuego and the Falklands.

Polyborus carunculatus, megalopterus, and *albogularis* are here treated as three subspecies of a single species, as previously advocated by Hellmayr and Conover (1949: 276-277), and adopted later by some students of South American birds (e.g., Olrog, 1963; Koepcke, 1964; and Johnson, 1965). (The name *megalopterus* Meyen, 1834, has priority over *albogularis* Gould, 1837, and should be used as the specific name, *contra* Hellmayr and Conover, 1949.) Other authors, however, have maintained the three taxa as separate species (e.g., Amadon, 1964: 14; de Schauensee, 1966; Brown and Amadon, 1968).

The divergence of opinion about the taxonomic status of these three taxa has hinged on two things: first, the striking interspecific adult plumage color differences, and secondly, the allopatry of the taxa. A third factor, namely the absence of intermediate specimens between any two of these forms, has been invoked by some authors to justify their treating the three as species. Brown and Amadon (1968: 371), for instance, stated: "the two [taxa] that are the most similar, *albogularis* and *megalopterus,* are not known to intergrade rather [sic] there seems to be a slight gap between their ranges, suggesting friction." A few specimens, however, do seem to be intermediate between *carunculatus* and *megalopterus* on the one hand, and between *megalopterus* and *albogularis* on the other, as discussed below.

The characters that vary from one to the other of the three taxa, *carunculatus, megalopterus* and *albogularis,* are: the amount of white at the tip of the primaries, the degree of curliness of the crest feathers, the extent of bare skin on the throat, and the coloration of the underparts. The two northern taxa, *carunculatus* and *megalopterus,* live in high Andean grassland and scrub above the timber line, at altitudes usually higher than 3000–3500 meters. Both of these forms are common birds where they live, and can be seen

daily in small groups or singly (personal observation). The populations of *caruncula tus* are geographically isolated from those of *megalopterus* by a hiatus that includes the low Andes of northern Peru, the depression of the Upper Marañon Valley and other valleys in northern Peru (see Fig. 4). Birds north of this gap (*caruncula tus*) have the throat and breast black with white longitudinal streaks or spots, and the abdomen white. South of the gap, birds (*megalopterus*) have throat and breast black without white spotting or streaking, and a white abdomen.

These morphological differences, considered in the light of the ecological barrier lying between the two taxa, might be interpreted as reflecting a period of geographical isolation during which differential selection acted on populations cut off from free gene flow. Absence of gene flow, however, seems surprising in view of the good flying abilities and the relative abundance of birds of this group. It is therefore noteworthy that Zimmer (1930: 248) found three adult males of *megalopterus* from Peru, all showing "an interesting progression in the direction of *caruncula tus*." Two of the three specimens (from Macate, Department Ancash, and Panao, Department Huánuco, see Fig. 4), have small, pale or whitish spots on the lower breast; the third specimen (from Junín, farther south) lacks breast spots. Zimmer's description of the three birds should be consulted for additional details.

These data seem to indicate that gene flow is indeed possible between Ecuadorian *caruncula tus* and Peruvian *megalopterus*. Further intensive collecting of these birds in northern Peru is badly needed. The total number of specimens of either *caruncula tus* or *megalopterus* from areas close to the barrier of northern Peru is low, so hybrid specimens might appear to be much rarer than they really are.

What about the situation between *megalopterus* and *albogularis?* The northern *megalopterus* is a common bird in the high Andean scrub vegetation of the Argentine-Chilean cordilleras. The southern *albogularis* seems to occur in *Nothofagus* forests rather than open vegetation types (see Olrog, 1948: 478; 1950: 520; Philippi *et al.*, 1954: 39). There seems to be a distributional hiatus (see Fig. 4) between the northernmost records of *albogularis* (in Neuquén, *fide* Olrog, 1963: 116) and the southernmost ones of *megalopterus* (in Talca, *fide* Johnson, 1965: 265). We do not know, however, whether this gap is real or not, because of the general scarcity of collections made in the "hiatus" area. In any

event, what is real is the fact that no ecological barrier interrupts the distribution of *megalopterus* and that of *albogularis* in the way the northern Peruvian low does between *megalopterus* and *carunculatus*. The situation seems therefore more complex ecologically, and deserves field study.

From these considerations, contact should be possible between *megalopterus* and *albogularis,* and if they are not reproductively isolated, gene flow should occur between them. In February, 1965, at 1950 m on Cerro Catedral, near Nahuel Huapi, Río Negro, Argentina (see Fig. 4), I observed two adult *Polyborus* that were attracted by a small garbage dump near the Refugio Lynch. One of them had the throat and breast black, in contrast with the white of the abdomen (*megalopterus*-like phenotype). The second had both a white throat and breast, with only the sides of the breast black, not forming a black pectoral band (*albogularis*-like phenotype). This observation might have been of a mixed pair, but unfortunately the birds could not be collected.

The possibility of mixed pairs and of offspring from them, seems to be shown by two adult birds that exhibit what appears to be intermediacy between *megalopterus* and *albogularis*. One of these birds, an adult male taken in February, 1896, in Chubut, southern Argentina, was described by Scott (1910) as *Ibycter circumcinctus*. The underparts of this specimen are as follows: the throat is white, followed by "a band of black below the throat patch more or less variegated by white on some of the feathers; this band is about an inch in width; lower part of the under neck pure white, the black of the sides of the neck confining the white of this region to a narrow area, widening into the pure white of the breast." This bird appears to be like a specimen of *albogularis* with a narrow black breast band. The second of these birds, an adult male from Nahuel Huapi (see Fig. 4), is mentioned by Hellmayr and Conover (1949: 277). This specimen (British Museum 99.1.27.229) has a distinct, interrupted breastband.

The same conclusion seems, therefore, to follow from these scanty data as from those on *carunculatus* and *megalopterus*: contact between *megalopterus* and *albogularis* seems a reality since at least two specimens are somewhat intermediate between the two taxa, and since birds from the two phenotypes were sighted together. Amadon, however, speaking of Scott's *"circumcinctus,"* said that it "may be a mutant rather than a true genetic intergrade" (1964: 15). This hypothesis seems unlikely to me. Since specimens of *albogularis* are relatively rare in museums, the two birds

with a black pectoral band represent a relatively high frequency of the black-banded phenotype, perhaps as many as 1 in 10 or 1 in 15—a number too high to be accounted for solely on the basis of recurrent mutation. A third possible interpretation would be that there is a polymorphism involving breast color. If this were true, then obviously *megalopterus* and *albogularis* should be considered members of the same species.

For the time being, I believe the best interpretation of the situation in this complex to be that the three taxa, although clearly differentiated morphologically as adults, have not achieved complete reproductive isolation, so that when two of them come in contact, whether across a barrier (*caruncula tus* with *megalopterus*) or not (*megalopterus* and *albogularis*), they produce hybrids. The taxonomic solution I propose in this paper is to consider all three taxa conspecific, although I realize that this lumping may be a little premature in view of the paucity of data. If additional study should reveal that hybridization is very limited, even though there may be plenty of opportunity for it to take place, then it would be justified to maintain the three taxa as species, although it would be necessary to emphasize that they are really semispecies: a truly intermediate stage in the speciation process.

DISCUSSION

The caracaras are interesting to the student of speciation, because they offer a variety of phenomena that are interpreted as intermediate in the process of species formation (see Table 3). They can be summarized as follows. In *Daptrius americanus,* the populations from southern Brazil may be geographically isolated from other populations farther north in South America. In *Polyborus plancus* can be seen phenomena of incipient speciation. Isolated populations, both insular (Tres Marías Islands, Cuba) and continental, exist, showing varying degrees of morphological differentiation. The most differentiated population (*lutosus*) was wholly insular, yet was of no evolutionary significance for further speciation since it is now extinct. The other insular populations, on the Tres Marías Islands and Cuba, are much less differentiated than *lutosus,* the Cuban one even being similar morphologically to the Florida population. On the continent, populations from northern South America (*cheriway*) are sufficiently differentiated from southern South American ones (*plancus*) for some ornithologists

TABLE 3

Stages of the speciation process in the caracaras

Species or semispecies	*Geographical variation*			*Secondary contacts*	*Members of a superspecies*	*Closest relative sympatric*
	Absent	*Clinal*	*Discontinuous (morphologically differentiated isolates)*			
Daptrius ater	+	−	−	−	−	+
Daptrius americanus	−	−	+[1]	−	−	+
Polyborus chimachima	−	+	−	−	−	+[2]
Polyborus chimango	−	+	−	−	−	+[2]
Polyborus plancus	−	−	+	+[3]	−	−
Polyborus australis	+	−	−	−	+	−
Polyborus megalopterus	−	−	+	+	+	−
Totals: 6	2	2	3	2	2	4

[1] *Daptrius americanus* has an apparently isolated population in southern Brazil

[2] *Polyborus chimachima* and *P. chimango* overlap in their distribution, yet are partially allopatric

[3] *Polyborus plancus* may exhibit secondary contact phenomena in South America

to have treated them as species. There is some evidence that (secondary?) hybridization takes place near the mouth of the Amazon where they come into contact.

The taxa of the *Polyborus australis* superspecies present another "stage" of the speciation process, in that one of the members of the superspecies, *australis,* is sufficiently distinct to be considered unhesitatingly as a species. The three remaining members, however, present interesting situations. In one instance, differentiation seems to have taken place across an ecological barrier (the low area of the northern Peruvian Andes), yet hybridization appears to occur in spite of this gap. In the second instance, no barrier is evident today, and some hybridization seems to occur. The southernmost taxon of this complex (*albogularis*) apparently meets *australis* in Tierra del Fuego.

In the *Polyborus chimachima* species-group, speciation is completed, and the two species overlap now over a considerable area, although they are allopatric over the major portions of their respective ranges. Finally, the two species of the genus *Daptrius* are so different morphologically and show so much sympatry that reconstruction of their history is impossible.

Although six of the seven species I recognize in the caracaras have extensive geographical distributions, the existing patterns of speciation, or incipient speciation, seem to indicate that multiplication of species has occurred mostly through the formation, and subsequent differentiation, of small or relatively small peripheral isolates. The present isolates of *Daptrius americanus* and *Polyborus plancus* are restricted to small areas around the periphery of the range of the species, and the geographical location of *Polyborus australis* relative to *Polyborus megalopterus* seems to suggest former peripheral isolation of the first named species. Differentiation within *P. megalopterus* does not seem to correspond as clearly to a pattern of isolation in peripheral areas, although the central populations (*megalopterus*) do have a much broader distribution than either the northern (*carunculatus*) or southern (*albogularis*) ones.

The previous summary of speciation in the caracaras shows that this process is most actively taking place along the Andes, where the various members of the *Polyborus australis* superspecies live. In the other, lowland, taxa, the speciation process is either completed (as in *Daptrius* or the *Polyborus chimachima* species-group) or is not as pronounced (*Polyborus plancus, Daptrius americanus*).

It is tempting to relate the apparently greater evolutionary activity in the Andean caracaras to the recent geological history of this cordillera. The high Andean grasslands and scrub habitats (páramo and puna) where *Polyborus megalopterus* now lives are undoubtedly the most recent environments of the Andes, and cannot be older than the latest phases of uplift, which brought the mountains to their present tremendous altitudes during the Plio-Pleistocene (see Childs and Beebe, 1963; Steinmann, 1930; Ahlfeld and Branisa, 1960; and Brüggen, 1950; for summaries of the geological development of the Andes). The differentiation within *P. megalopterus* most probably occurred during the Pleistocene glaciations, although to attempt the dating of such processes is almost complete guess work. However, if we recall that during glacial episodes, the temperature depression lowered the altitude of the upper vegetation zones, where *P. megalopterus* lives, then it becomes possible to envision the separation of a northern isolate (proto-*carunculatus*) in Ecuador at interglacial time, when the altitudinal raising of this treeless zone occurred, thus increasing the effectiveness of a natural barrier such as the Upper Marañon Valley and northern Peruvian low for birds living on either side of it. The isolation of *carunculatus* from *megalopterus,* or, rather, of proto-*carunculatus* from proto-*megalopterus,* might, then, have happened during an interglacial. It is, of course, not possible to suggest which of the several interglacial periods was responsible for such an event.

Similar glacial-interglacial oscillations may have permitted the separation of proto-*megalopterus* and proto-*australis* in extreme southern South America. During the maximum glacial, extreme southern South America was covered with an ice-sheet (Caldenius, 1932; Polanski, 1965) which probably forced Andean biota to "retreat" considerably northward. At the same time, however, the Falkland Islands were left unglaciated, and, furthermore, were of greater area than today because of a concurrent lowering in sea-level. It seems therefore possible that during the maximum glaciation the southernmost populations of the stock common to *megalopterus* and *australis* remained on a Falkland refuge, where they were geographically isolated from mainland populations by the ice barrier, added to the sea barrier. If such a separation did indeed take place during the maximum glaciation, which is attributed to the late Pleistocene (Würm or Wisconsin) (see Polanski, 1965), then the splitting of an ancestral stock into the modern *australis* (having evolved from a population in a southern insular refuge)

and *megalopterus* (having remained in Andean Patagonia, but considerably farther north than its present-day southernmost limit) may have taken place as recently as 50,000 to 80,000 years ago. Of course, it is also possible that the original separation took place during an earlier, somewhat less extensive, glacial episode, but since the maximum glaciation apparently obliterated earlier remains, it is futile to speculate any further about the possible course of this event.

ACKNOWLEDGMENTS

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BREVIORA

Museum of Comparative Zoology

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On new species in a new earthworm genus from Puerto Rico[1]

G. E. Gates[2]

ABSTRACT. A new genus of earthworms, *Estherella* (family Glossoscolecidae), with new species *montana* (type species) and *nemoralis*, is described from Puerto Rico, and its remarkable structural modification is discussed.

A seemingly impossible evolutionary modification was shown by several worms received 25–30 years ago. Immaturity, amputation, maceration, and paucity of specimens prevented completion of species descriptions to desired standards. Unfortunately subsequent material never became available. Various attempts to secure it were futile. This contribution now is proferred in hope of awakening interest in: 1) An evolutionary development that some zoologists categorically maintain is impossible. 2) The mostly unknown earthworm faunas of Caribbean Islands.

Glossoscolecidae

Estherella gen. nov.

Definition. Digestive system, with a gizzard in iii, three pairs of calciferous glands in v–vii, each gland sausage-shaped, vertically placed alongside gut, with a short duct from dorsal end opening into esophagus just lateral to the supra-esophageal vessel, intestinal origin in region of xix–xx, with a lamelliform typhlosole, without caeca and supra-intestinal glands. Vascular system, with a single dorsal trunk aborted in front of hearts of iv, complete ventral and subneural trunks, the latter adherent to parietes, a supra-esophageal trunk in v–xiv, paired latero-esophageal trunks

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in iii–ix with connectives to supra-esophageal in v–vii. Hearts, in iv–vii lateral, in viii latero-esophageal. Nephridia, holoic and vesiculate. Nephropores, obvious, in a regular longitudinal rank on each side in region of *CD*. Pigment, none. Septa, present from 3/4. Prostomium, none, replaced by a protrusible proboscis. Setae, eight per segment, in regular longitudinal ranks.

Quadrithecal, spermathecae adiverticulate, pores in region of *CD*, at 5/6–6/7.

Type species, *E. montana* n. sp.

Distribution. Puerto Rico.

Estherella montana sp. nov.

Puerto Rico, El Yunque Mountain. Wet cloud forest at ± 2500 feet, May 1938, 3–0–0. P. J. Darlington per G. E. Pickford. (Mus. Comp. Zool.) About 2200 feet, an anterior fragment, C. W. Richmond & L. Stejneger. (U. S. Natl. Mus.)

External characteristics. Length, 50–60 mm (juveniles), 175 mm (posterior amputee of 148 segments). Diameter, 4 mm (juveniles), 12 mm (amputee). Segments of 54 mm juvenile, 188. Color, white (long alcoholic preservation). Peristomium, much shorter than ii but of about the same appearance externally as subsequent segments. Intersegmental furrows, distinct. Segmental length, gradually increasing posteriorly to region of vii–ix. Secondary annulation, a presetal and a postsetal secondary furrow in each of ix–xxvi, postsetal secondaries unrecognized behind xxvi. Nephropores, obvious, present from ii, well behind intersegmental furrows but usually less than half way toward segmental equators, at or near *C*. Setae, paired, ventral couples first certainly recognizable in v, lateral couples in region of xv, in region of xxx *CD* slightly $< AB$ much $< AA < BC$, posteriorly AA *ca.* $= BC$, still further back $AA > BC$. Dorsal pores, none.

Quadrithecal, spermathecal pores, minute, superficial, in *CD*, at 5/6–6/7. Other genital apertures, unrecognizable. Genital tumescences, transversely and shortly elliptical, indistinctly delimited, each with two circular areas of epidermal translucence at center of which is a follicle aperture, *a,b*/xv–xxiv. Region of *AA*, rather deeply depressed through xv–xxiv.

Internal anatomy. Septa, 4/5–13/14 thickly muscular to muscular, funnel-shaped, large, apices well posteriorly, 14/15 and following septa slightly strengthened by muscular fibers. Septum 3/4, a delicate transparent membrane bearing on its posterior face

one pair of nephridia and on its anterior face two other pairs of tubules, with insertion on gut immediately behind gizzard. Pigment, if once present in body wall, completely leached by preservative. A large, empty canal, ellipitical in cross section, apparently completely circumferential, in anterior portion of body wall in each of i–x. Canal size, decreasing posteriorly. Brain, in ii. Nerve cord sheath, massively muscularized (Fig. 1) anteriorly but so as to leave a greyish translucent line visible at mD and mV in the cord between segmental ganglia (Fig. 2).

Buccal cavity, in i dorsally of small juveniles, seemingly provided, though only temporarily, with a suckerlike pad somewhat resembling the withdrawn and depressed condition of the prostomium in various megadriles, in ii dorsally with a circular aperture into a tunnel containing a presumably protrusible proboscis 1–2 mm long. Gut from level of intersegmental furrow 2/3 to septum 4/5, *ca.* 30 mm long, sigmoid, comprising a pharynx (4 mm long), a bulb (5 mm thick dorsoventrally and with a glandular chamber anteriorly), a slender esophagus (14+ mm long) with closely crowded, low longitudinal ridges on its inner wall, a sort of conical crop (5 mm long) with circular ridges on its inner wall, and a powerful gizzard (6 mm long) referable to iii.

Calciferous glands, in contact with each other mesially under the gut, in vii ducts longer but concealed by adherence of 7/8 (near apex of its funnel) to the gut. Typhlosole, present from region of xxiv–xxvi, 10 mm high (3 mm, small juvenile), rolled up on itself like a scroll, ending in region of 125th segment (132d of 188). Lateral typhlosoles, not lamelliform, rounded and protuberant ridges in first one or two typhlosolar segments.

Ventral blood vessel, high up in coelom and near gut in v–xi at least. Extra-esophageals, interconnected by a transverse vessel just in front of 4/5 and just under the ventral trunk, anteriorly passing up and branching among nephridia associated with 3/4. Supra-esophageal, with a large branch on each side in v and vi that bifurcates, one branch to a calciferous gland near the duct, the other passing down along anterolateral aspect of the gland to an extra-esophageal trunk, connected also with extra-esophageals by a pair of vessels, seemingly on posterior face of 7/8 but mostly within the septum. Hearts, of iv–vii slender and lateral, of viii apparently latero-esophageal—posterior bifurcations to dorsal trunk slender and empty, anterior branches filled with blood and obviously joining the supra-esophageal.

Nephridial ducts (of anterior segments), passing down through longitudinal muscle layer and then turning forward to cross the circumferential intra-parietal canal, thence anteriorly widened and with more opaque (muscularized?) wall.

Spermathecae, rudimentary, adiverticulate, within the longitudinal muscle layer.

Remarks. Small juveniles are assumed to be of the same species as the large worm from the same mountain.

Rudimentary state of the spermathecae and absence of macroscopically recognizable gonads, funnels, and seminal vesicles, indicate that even the large worm was juvenile though maximum diameter for the species may have been attained.

The parietal insertion of the delicate septum 3/4 had become unrecognizable presumably as a result of pinning out the specimen after a longitudinal incision had been made near the mid-dorsal line.

Any connection between nephridial ducts and the circumferential intraparietal canals would have been too small to recognize in dissection, and microtome sections were unsatisfactory. The canals were crossed diagonally by delicate fibers (or septa?). Similar canals had been observed at least once before, but records were destroyed during World War II.

Abortion of dorsal trunk in front of hearts of iv and posteriorly in that segment was found in each dissected specimen considered herein. That and other characters already mentioned in the generic definition do not need mention again in species descriptions.

Photographs of nerve cord sections were provided by Prof. E. Carpenter.

E. nemoralis sp. nov.

Puerto Rico. Luquillo Forest (Caribbean National Forest), La Mina Recreational Area, at 1800 feet, February 22, 1947, 2 macerated specimens (several younger specimens possibly of the same species, also macerated.) R. Kenk. (U. S. Natl. Mus.)

External characteristics. Length, 250 mm. Diameter, 9 mm. Segments, 220 (at 195/196 a tail regenerate with terminal anus). Color, possibly red originally, even after long alcoholic preservation dorsum with a slight reddish tinge except in regenerate. Nephropores, obvious, present from ii, in *CD*. Setae, closely paired throughout, $AB = CD$, $AA > BC$, DD *ca.* $= \frac{1}{2}$C, ventral

couples of some segments modified (? but genital tumescences not recognized).

Clitellum, perhaps represented by a dark brown coloration in xv–xxii, xxiii/eq, which is conspicuously lacking in a small area around each nephropore, no epidermal tumescence recognizable. Quadrithecal, pores minute, superficial, each at center of a small tubercle at *C* and at or immediately in front of 5/6–6/7. Female pores, postsetal in *AB* of xii(?).

Internal anatomy. Septa, 4/5–6/7 very thickly muscular, a transparent, funnel-shaped membrane bearing three pairs of nephridia inserted on the gut just behind the gizzard almost immediately in front of 4/5 presumably being 3/4, 7/8 lacking or else inserted on parietes over intersegmental furrow 8/9.

Calciferous glands, without a central lumen but with a honeycomb appearance in cross sections, each with a small distal appendage.

Supra-esophageal, bifurcating posteriorly in xiv, giving off two pairs of vessels, one immediately behind the other and both just in front of the septum in each of v–vii, the posterior of each pair giving off branches to the calciferous gland and ventrally joining the extra–esophageal trunk of its side, the anterior vessels passing onto stalks of calciferous glands and down through the glands into the terminal appendages. Extra-esophageal, first visible in region of 3/4 as a result of union of several large vessels, with several branches to each calciferous gland of its side. Subneural trunk, large, zigzag-looped, closed ends of loops visible beyond both sides of the nerve cord, bifurcating just in front of subpharyngeal ganglion (one specimen) or in region of xvii (one), each branch passing anteriorly in a zigzagged course lateral to the cord but connected with its twin on the opposite side by numerous transverse vessels. Ventral trunk, high up in coelom as in *E. montana.* Hearts, large, two pairs, possibly latero-esophageal and attributable to viii–ix (?).

Testis sac (or sacs?) filled with coagulum, surrounding or including hearts belonging in viii (?).

Spermathecae, sessile, ducts confined to body wall, ampullae small, protruding only slightly into coelomic cavities of vi and vii.

Remarks. Intersegmental furrows, in spite of the maceration, are distinct, and septa 4/5–6/7 are inserted on the parietes directly over intersegmental furrows 4/5–6/7.

Thickness of the subneural trunk is greater than that of the nerve cord even in regions of segmental ganglia.

The cuticle was loose and setae had been pulled out of their follicles.

Repetition in the description of characters shared identically with *E. montana* seems unnecessary. Mention should be made of the fact that a proboscis and circumferential parietal canals were not seen.

This species is distinguished from *E. montana* by absence of the marked muscularity in the nerve cord sheath.

Estherella sp.

Puerto Rico. Luquillo Forest (Caribbean National Forest), La Mina Recreational Area, 1800 feet, February 22, 1947, 1 macerated specimen. R. Kenk. (U. S. Natl. Mus.)

External characteristics. Size, 150 by 7 mm. Nephropores, obvious, present from ii, in *CD*. Setae, paired throughout (ventral couples modified in some clitellar segments?).

Clitellum, xv–xxii (and xxiii?). Tubercula pubertatis, longitudinal bands of translucence, just lateral to *B*, each demarcated laterally by a deep furrow. Female pores, postsetal in *AB* of xii(?).

Internal anatomy. Male funnels, one pair, iridescent, imbedded in coagulum apparently also containing hearts of viii and possibly in sacs (or a testis sac?). Spermathecal ampullae, spheroidal, without spermatozoal iridescence, slightly protuberant into coelomic cavities from the angles of septal insertions and parietes.

Remarks. Setae had been pulled out of their follicles as in the types of *nemoralis*. Gonads and female funnels were not found. Structure, so far as could be determined, is the same as is shared by the two preceding species.

The reason for anticipating a third species is the maturity at a size smaller than is expected for the other two.

SYSTEMATICS

Cephalization has had little attention from oligochaetologists and perhaps least of all in connection with a family in which one manner of evolutionary modification seemingly had its most extensive, as well as perhaps least appreciated development.

Metamerism in oligochaetes sometimes has been said to be homonomous, *i.e.*, similar throughout the body. Typically, the soma is in anteroposterior segments, each of which, at least in earlier stages of evolution, has four pairs of setae, a pair of

nephridia, and a section of the gut. Such a segment is demarcated externally from each of its two contiguous neighbors by intersegmental furrows, circumferential lines where the epidermis is thinnest. Internally, a segment is delimited by transverse partitions, the intersegmental septa. The latter, typically, are in exactly the same anteroposterior levels as the intersegmental furrows. Peristomium and periproct, according to such definitions, are not segments, though for practical purposes are counted as such.

Differentiation in a relatively short anterior portion of the soma of special digestive organs such as gizzards, calciferous glands, etc., and localization of gonads are aspects of oligochaete cephalization so universal as not even to have been thought to be involved. More usually considered were abortions, as of follicle and nephridial anlage, and disappearance of septa and intersegmental furrows, *i.e.*, those structures existence of which enables recognition of segments. Slight (or at least seeming) displacements of septal insertions on the parietes have been known for some time. Recognized but recently (Gates, 1943: 92) was a seemingly posterior dislocation of the parietal insertion of septum 9/10, in *Pontoscolex corethrurus* (Müller, 1857), to a position over site of intersegmental furrow 10/11. Failure to recognize that dislocation was responsible in part for assignment of certain organs in systematic descriptions to wrong segments. How many other errors of that sort were made in past characterizations of glossoscolecids remains to be learned.

Appearance of deep, secondary, and even tertiary furrows hardly distinguishable from the primary intersegmentals, in association with abortions of setae and nephridia, also has been responsible for errors in determination of organ locations. Such mistakes are unfortunate, as knowledge of exact organ position along the anteroposterior axis is of first importance for megadrile systematics and phylogeny. Absence of data as to segmental location of the gonads in the Puerto Rico species is not so regrettable as would formerly have been thought since it is now known that "andry" often, and sometimes even "gyny," does vary intragenerically.

Fortunately, the worms now under consideration, in spite of the poor condition, are free of external modifications that might lead to wrong determinations of organ locations. Setal follicles, to be sure, have been aborted in some of the anteriormost segments, but compensation is provided by the nephropores which not only are all present but also are obvious. Secondary and

tertiary furrowing is lacking, and the anterior segments are clearly demarcated by unmistakable intersegmental furrows. The first two segments have the normal appearance of externally exposed epidermis. No evidence was found for the existence of an actual pre-oral vestibule comprising one or two rudimentary segments no longer exposed regularly to the external environment. Furthermore, the unusual condition next to be discussed characterizes every individual of two, or possibly even three, species. Individual abnormality or defective anterior regeneration accordingly cannot be invoked as was contended when a single Panama specimen was described (Gates, 1968) with a similar condition.

The powerful gizzard, being in front of a membrane that, because of nephridial relationships, must be regarded as septum 3/4, is unusually anterior. With the single exception of the above-mentioned Panama species, a megadrile gizzard has not hitherto been found in front of segment v and often is further back in the esophagus. Other organs also are too far forward. The last pair of hearts is in viii, whereas the first pair of real hearts usually is in ix. Calciferous glands are present in v only in the Panamanian *Thamnodriloides yunkeri* Gates, 1968. Lastly, testes are at least two segments in front of where they would normally be expected.

Accordingly, much more is involved than forward displacement (homoeosis) of a single organ but rather a condition in which all organs of the cephalic region from gizzard posteriorly are three segments in front of their expected positions (regional homoeosis).

An initial or very early stage in an evolutionary development that may have reached its climax in the Puerto Rico and Panama worms is provided by *P. corethrurus*. In that species an intersegmental furrow between the first and second segments has disappeared along with the prostomium. The now rather flaccid fusion metamere is small. Proof of what happened is provided in many specimens by retention of the setae belonging to ii which are now near the first intersegmental furrow that morphologically is 2/3. With loss of those setae, as in some individuals of the species, the gizzard would have to be referred to v instead of vi. Organs behind the gizzard also would be one segment anterior to their usual position. Abortion of two further segments by the same process under way in *P. corethrurus* would provide the regional homoeoses of the Puerto Rico and Panama genera. Although body wall and associated nephridia were markedly reduced or deleted, the digestive system was not correspondingly shortened.

On the contrary, there has been so much elongation as to require very considerable enlargement of associated septa into posteriorly directed funnel-shapes. What happened in the nervous system may prove to be interesting also.

Although homoesoses are identical, the digestive systems and especially structure of the calciferous glands show that the two fore-shortened genera are not closely related. Puerto Rican worms may have evolved from a stock with calciferous glands in viii–x. Genera so characterized are unknown. Related forms should be sought to the south as the glossoscolecids evolved in tropical South America. Puerto Rico now appears to be the northern limit of generic endemism.

Completion of a development somewhat like that now under way in *P. corethrurus* may be responsible for attribution of testes in *Thamnodrilus matapi Righi*, 1969, to segments ix and x instead of the expected x and xi.

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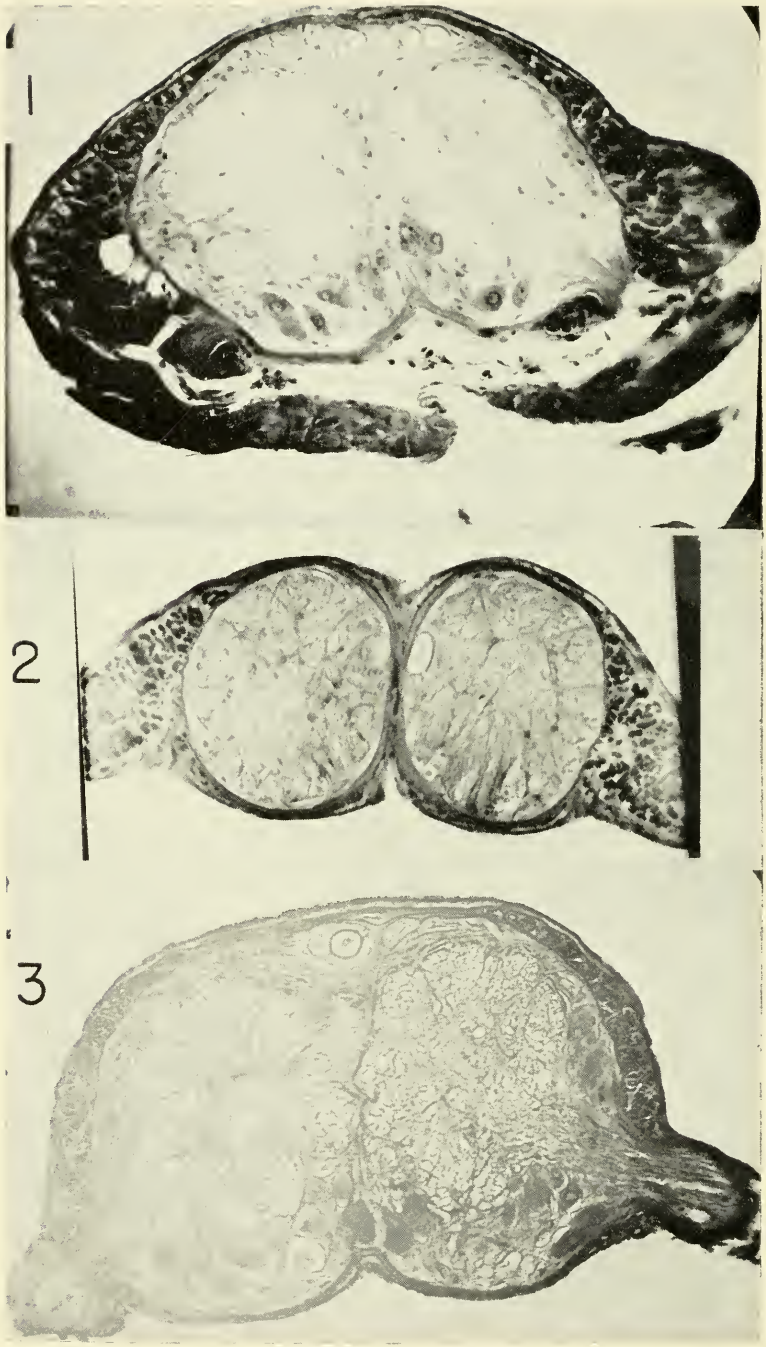
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Figure 1. *E. montana.* Transverse section of nerve cord anteriorly to show muscularization of the sheath.

Figure 2. *E. montana.* Transverse section of nerve cord anteriorly to show the condition responsible for the appearance of a greyish translucent line at mD and mV.

Figure 3. *E. montana.* Transverse section of nerve cord anteriorly to show giant cells ventrally.

BREVIORA

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A review of the fossil Pelomedusidae (Testudines, Pleurodira) of Asia

Roger Conant Wood

ABSTRACT. The taxonomic status of the three Asiatic chelonian genera that have been described as pelomedusids is reviewed. Of these, *"Podocnemis" indica*, although possibly a member of the family, is so poorly known that familial assignment is not presently possible. *Carteremys leithii* and *Shweboemys pilgrimi* both appear to be valid palomedusid species. On the basis of new material *S. pilgrimi* is redescribed and, in addition, a new species of this genus from the Miocene of Baluchistan, *S. gaffneyi*, is proposed.

INTRODUCTION

Living pelomedusid turtles are restricted to sub-Saharan Africa, Madagascar, and South America. But paleontological evidence indicates that pelomedusids formerly had a much more cosmopolitan distribution; fossil representatives of this family occur in North and South America, Europe, Africa, and Asia.

The purpose of the present paper is to review the extinct Asiatic chelonian genera that have been described as pelomedusids as well as to put on record two new fossil pelomedusid skulls from Asia, one referable to *Shweboemys pilgrimi* and the other representing a new species of the same genus.

Abbreviations used in this paper are:
ANSP—Academy of Natural Sciences, Philadelphia
BMNH—British Museum (Natural History)
GSI—Geological Survey of India
MCZ—Museum of Comparative Zoology, Harvard University

I have not seen the material described by Lydekker, Swinton, and Williams that is contained in the collections of the Geological Survey of India, but it is for the most part well figured in the literature. Photographs of the type of *Shweboemys pilgrimi* Swinton have been available.

PREVIOUSLY DESCRIBED ASIATIC PELOMEDUSIDS

Very few fossil pelomedusids have been described from anywhere in Asia, and none of these is particularly well known on the basis of published material.

"Podocnemis" indica Lydekker 1887. This species was described on the basis of a fairly complete carapace and on some miscellaneous plastral fragments found at Nila in the Salt Range of West Pakistan. Lydekker was uncertain about the age of *"P". indica* but concluded (1887: 59) that it was probably of ". . . lowest eocene . . . and may . . . correspond to the Cernaysian stage of Reims, and the Puerco group of the United States." Since it is now generally recognized that the Cernay beds are of late Paleocene age and the Puerco beds of early Paleocene age, *"P." indica* may actually be of Paleocene rather than Eocene age. Both Paleocene and early Eocene deposits occur in the Tertiary sequence of the Salt Range (Krishnan, 1960: 494), and too much uncertainty exists as to the exact stratigraphic horizon from which the only known specimen of *"P." indica* was obtained to resolve the question of its age beyond all doubt. Invertebrates found in association with the two chelonians (*"Podocnemis"* and *Hemichelys*) described from this locality ". . . indicate that the bed in which they were found is either of marine or estuarine origin; and this is confirmed by the chelonians, one of which is covered with the 'spat' of oysters, while sharks' teeth are embedded in the matrix of the other" (Lydekker, 1887; 59–60).

Preservation of the carapace of *"P." indica* is rather poor; Lydekker noted (1887: 60) that ". . . both specimens [from Nila] . . . were in a much broken condition, and . . . required all [the preparator's] skill to render them fit for description." Lydekker's restoration of the carapace (1887, plate 13) indicates that its most distinctive feature is a peak along the midline of the neurals, with the pleurals on either side apparently sloping away flatly rather than on a curve. The nuchal bone appears to be unusual in that its postero-lateral sides are considerably longer than its antero-lateral ones. The nuchal is rather small and does not transgress the lateral boundaries of the first vertebral scute. There are seven neurals; the first five are all longer than broad, whereas the last two are broader than long. Two pleurals (the seventh and eighth) meet in the midline between the last neural and the suprapygal. No indentation occurs at the midline along

the anterior margin of the carapace and a cervical scute[1] is lacking. Whereas the first vertebral is nearly twice as wide as it is long, the second and third vertebrals are both longer than broad. Lydekker estimated (1887: 63) that the overall length of the carapace must have been approximately 35 inches (87 centimeters), exceptionally large for a fossil pelomedusid. Critical taxonomic evidence, such as whether or not the pelvis was fused to the shell, the presence or absence of mesoplastra, and the scute pattern on the anterior plastral lobe, is not preserved. Consequently, there is no assurance that *"P." indica* is actually a pelomedusid, let alone a member of the genus *Podocnemis*. Nevertheless, its midline ridge and straight loping sides are somewhat reminiscent of the carapace structure of a recently discovered shell of *Shweboemys* from Egypt (see p. 00), and the number, shape, and arrangement of its neurals is typical of many pelomedusids, as is its lack of a cervical scute. Therefore, it does not seem altogether unlikely that *"P." indica* may represent the remains of some kind of pelomedusid, although it probably is not a member of the genus *Podocnemis*. Until more complete specimens of this taxon are discovered, I do not think that a better identification of this specimen is possible than Pelomedusidae? *incertae sedis*.

Carteremys leithii (Carter 1852). A second Asiatic pelomedusid taxon, *"Hydraspis" leithii,* was recovered from Intertrappean beds near Bombay, India. Some uncertainty exists as to the age of these sediments. Lydekker (1887: 60) regarded them as "lower eocene." Referring to the age of the volcanics within which the Intertrappean beds occur, Wadia (1953: 302) stated that " . . . it is quite apparent that the Deccan Traps cannot be older than the Danian stage of the uppermost Cretaceous [now Paleocene], while . . . they cannot be much younger than the Eocene." According to Krishnan (1960: 483–486), paleontological evidence afforded by fossils contained within the Intertrappean beds is not particularly helpful for dating, but on other grounds he concluded that the Deccan Traps ranged in age from late Cretaceous to, perhaps, Oligocene. Robinson (1970: 245) has expressed similar views, stating that the Intertrappeans are ". . . probably mainly early

[1] I have here adopted the term suggested by Zangerl (1969: 315) for this particular scute to avoid the confusing redundancy arising from the conventional procedure of referring to both it and the underlying bone as the nuchal.

Tertiary in age. . . ." Since the Intertrappeans of the Bombay region are confined to the upper part of the Deccan Traps (Pascoe, 1964: 1385), their attribution to the Eocene would not be unreasonable. Krishnan (1960: 482), Pascoe (1964: 1385) and Robinson (1970: 245) all agree that the Bombay Intertrappeans were laid down in fresh water, Pascoe further suggesting (1964: 1386) that the depositional environment was a shallow marsh.

Carteremys leithii was a small species; the only two complete carapaces for which measurements have been recorded are 7¼ and 8 inches (18–20 centimeters) in length (Carter, 1852: 187; Williams, 1953: 6). Carter's original description was based on material that is now unfortunately lost (Williams, 1953: 2). Only three other specimens that can be referred to this species with reasonable confidence have subsequently been discovered (Williams, 1953: 6, and plate 3). The total number of neurals is uncertain, although there are at least five. Evidently no cervical scute was present, and the first vertebral was much smaller than the second. The outer surface of the shell is covered with fine sculpturing. In several respects the plastron is quite distinctive: it is relatively narrow, with a semicircular anterior lobe projecting well forward of the front of the carapace; between the broadly rounded xiphiplastral tips is a very shallow anal notch, not comparable in its shape to those of any pelomedusid with which I am familiar; and the outlines of the pelvic scars on the xiphiplastron are also unusual. In spite of Williams' suggestion (1953: 4) that small, laterally placed mesoplastra, a characteristic pelomedusid feature, may have been present, there is no conclusive evidence bearing on this point. None of the three existing specimens (all belonging to the collections of the Geological Survey of India) is sufficiently complete to demonstrate the presence or absence of these structures (Williams, 1953: 6). Trapeziform gulars were widely separated by an extremely broad intergular scute that extended posteriorly to the humero-pectoral sulcus and thus prevented the humerals from meeting in the midline also. The most notable feature of the skull is the extensive emargination of the roof from behind, a condition typical of most pelomedusids. A well-developed jugal-quadratojugal bar is present. Although the extremity of the mandibular rostrum was broken off in the material Carter described, it is clear from what was preserved that there must have been a broad, robust symphysis at the midline of the lower jaw.

Long regarded as a chelid, *"Hydraspis" leithii* was eventually redescribed and designated as the type of a new pelomedusid genus by Williams (1953: 3–4). A combination of several characters—the absence of a cervical scute, the relative proportions of the first and second vertebrals, the remarkably large intergular, and the lack of a parieto-squamosal arch combined with the presence of a jugal-quadratojugal bar—led Williams to conclude that this species could not be a chelid. These characters, together with the inferred existence of small, laterally placed mesoplastra, persuaded him that *Carteremys* was in fact a pelomedusid. On the basis of the data presented in Table 1, I agree with Williams' conclusion. If we disregard for a moment the question of whether or not mesoplastra were present in *Carteremys*, then we see that for all the characters tabulated, this genus and pelomedusids agree. In contrast, none of the other families share more than two characters with *Carteremys*. This comparison strongly suggests that *Carteremys* is a pelomedusid. Should it eventually be possible to determine that *Carteremys* had mesoplastra, the evidence would overwhelmingly favor this determination.

Lydekker (1890: 22–23, fig. 2) referred an epiplastral fragment, probably from Intertrappean beds and therefore possibly of Eocene age, to *"Hydraspis" leithii*. Differing from *Carteremys* in size and in gular-intergular proportions, this specimen may well represent an unknown taxon, but too little is known of it to permit useful discussion.

Shweboemys pilgrimi Swinton 1939. The type, and until now only known specimen, of this species is a partial skull of Pliocene or Pleistocene age from Burma (Swinton, 1939). Swinton believed that nasal bones, although not preserved on the specimen he described, must have been present originally. Were this supposition true, his placement of the genus in the Pelomedusidae would be suspect because one of the diagnostic characters of the family is the absence of nasals (*cf.* Romer, 1956: 515). Evidently Swinton was either unaware of the significance of this character or else he did not consider it to be of great importance; at any rate, he did not discuss its bearing on taxonomy. Nevertheless, other observations led him to conclude (1939: 551) that *Shweboemys* is a pelomedusid: "In brief, the interest of the specimen is that in superior and lateral aspect there is little to distinguish it from the genus *Podocnemis*, while in palatal view it has much similarity to *Stereogenys*. There is no doubt that it

TABLE 1

Various characters of *Carteremys leithii* compared with those of several chelonian families with which it shares one or more in common.

Characters	*C. leithii*	*pelomedusids*	*chelids*	*dermatemydids*	*testudinids*
Intergular present	yes	yes	yes	sometimes	no
Cervical present	no	no	usually	yes	usually
Mesoplastra present	uncertain	yes	no	no	no
Temporal roof of skull emarginated from behind	yes	yes	rarely[1]	yes	yes
Jugal-quadratojugal bar across the cheek region	yes	yes	no	no	usually

[1]Only in the Australian genus *Chelodina* has the parietal-squamosal bar normally present in chelids been lost.

differs from both genera and is a new form belonging to the family Pelomedusidae."

NEW ASIATIC PELOMEDUSID MATERIAL

The recent recognition of a second, slightly more complete specimen of *Shweboemys pilgrimi* by Mr. C. A. Walker in the collections of the British Museum (Natural History) has provided new information which confirms Swinton's familial determination. Further supporting evidence is furnished by the new species of *Shweboemys* from the Miocene of Baluchistan (West Pakistan) described below. In addition, recent Yale University paleontological expeditions to the Fayum Depression of Egypt have produced conclusive evidence showing that *"Podocnemis" antiqua* Andrews 1903 from the late Eocene Qasr el-Sagha Formation is referable to *Shweboemys*. A detailed description of this species, the only one represented by both skull and shell material, is being prepared for publication elsewhere, but I include the diagnostic characters of its shell in the emended diagnosis.

Shweboemys Swinton 1939

Type species. Shweboemys pilgrimi Swinton 1939.

Emended diagnosis. Skull with broad secondary palate formed by medial expansion of maxillae and palatines, with narrow median cleft extending posteriorly from behind premaxillae; outer border of palatines not parallel to midline axis, but diverging from it at an angle of approximately thirty degrees; laterally projecting. prominent ectopterygoid processes; enlarged carotid channels; basisphenoid not covered by pterygoids ventrally. Carapace cordiform in outline, tapering to a point posteriorly; pleurals flat rather than curved, sloping away from continuous midline ridge at gentle angle; ventral surface of plastron completely flat; anterior lobe of plastron very short and semicircular; posterior lobe narrower and approximately one and one-half times longer than anterior; outer margin of posterior lobe straight rather than curved, slanting inward toward rear.

Referred species. Shweboemys antiqua (Andrews) 1903, *S. gaffneyi* sp. nov.

Distribution. Late Eocene, Fayum Depression, Egypt; early Miocene, Bugti Hills, West Pakistan; Pliocene or Pleistocene, Burma.

The skull of *Shweboemys* is very similar to that of *Stereogenys* but differs in several significant respects: the pterygoids do not completely cover the basisphenoid ventrally; the lateral margins of the palatines are not parallel to the midline axis; and the secondary palate is less elongate, not extending back as far as the ectopterygoid processes.

Swinton's decision to base a new pelomedusid genus and species on his Burmese specimen was founded on his belief that the skull combined features of both *Podocnemis* and *Stereogenys* without being more like one than the other (see p. 5). That the palatal structure of *Shweboemys* is very similar to that of *Stereogenys* and different from that of *Podocnemis* is indisputable, but Swinton's remark that the dorsal and lateral aspects of *Shweboemys* are virtually identical to the comparable regions of *Podocnemis* and unlike those of *Stereogenys* is an overstatement. Swinton (1939: 550) evidently compared the type of *Shweboemys pilgrimi* only with Andrews' original description (1901: 442) of the type skull of *Stereogenys cromeri,* which is somewhat crushed dorso-ventrally in the facial region as Andrews himself noted (1901: 443n). Another specimen (BMNH—R.3189), which Andrews later (1906: 301 and plate 25, fig. 1) referred to this species, is not flattened[1] and reveals that virtually all of the characters used by Swinton (1939: 550) to differentiate *Stereogenys* from *Shweboemys*—the relative positions of the orbits and external nares, shape of the orbits, and breadth as well as flatness of the skull—are artifacts of preservation rather than taxonomically significant features. Swinton also claimed (1939: 550) that the facial bones of *Stereogenys* were more slender than those of *Shweboemys.* The difference in thickness is easily explained, however. The type of *Shweboemys pilgrimi* is considerably larger than that of *Stereogenys cromeri* (12.5 *versus* slightly more than 8 centimeters from the snout to the occipital condyle) and the thicker bones merely reflect greater size. In dorsal and lateral aspects, therefore, the skull of a *Shweboemys* does not resemble that of *Podocnemis* more than it does that of *Stereogenys.*

[1] If anything, in terms of distortion, this skull may perhaps be somewhat compressed laterally.

Shweboemys pilgrimi Swinton 1939
(Plates I, IIA, IIIA, IVA)

Type. GSI 17255, an incomplete skull. The original description of this specimen was accompanied only by some rather crude sketches (Swinton, 1939, text-figures 1 and 2). Photographs of the type showing comparable views are therefore reproduced as Plate I.

Hypodigm. The type and BMNH—R. 8432, a slightly more complete skull lacking the anterior portions of the premaxillae, both ectopterygoid processes, part of the left and all of the right paroccipital process, and, to whatever extent it may have been developed, the supratemporal roof.

Horizon and locality. Pliocene or Pleistocene, Irrawaddy beds, one mile NNE of Mauktet, Shwebo District, Burma.

Swinton's determination of a Pliocene age for the type (1939: 548) is questionable because he failed to state—perhaps because the information did not exist—at what level within the Irrawaddy sediments the specimen was found. It is generally recognized that there are two faunal horizons within the Irrawaddy beds, a lower one of Pliocene age and an upper one of Pleistocene age (Stamp, 1922: 498; Colbert, 1938: 267; Krishnan, 1960: 554). Undetermined chelonian remains have been reported from the lower beds near Yenangyaung (Stamp, 1922: 498), but these have never been formally described. Fossil turtle fragments have also been recovered from the upper Irrawaddy beds (Colbert, 1943: 417). One of these, MCZ 1890 (MCZ 6305 in Colbert) represents the left epiplastron of a very large tortoise while another (ANSP 14644), according to Colbert, may be a trionychid. No pelomedusid remains have been recognized among these specimens. Whether the Irrawaddy beds of the Shwebo District, whose administrative center, the municipality of Shwebo, lies some 130–140 miles to the northeast of Yenangyaung, represent only the upper part or the lower part of this sedimentary unit, or a mixture of both, is unknown. Consequently, the absence of any reasonably precise stratigraphic data for Swinton's specimen does not permit a decision as to its age. Unfortunately, nothing is known about the provenance, other than "Burma," of BMNH—R. 8432. Its morphological identity with the type of *S. pilgrimi* leads me to believe that the two skulls are of essentially the same age.

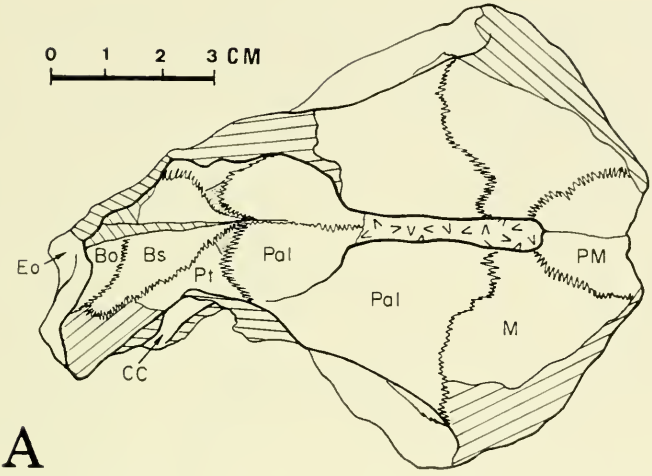
Emended diagnosis. Interorbital width slightly greater than diameter of orbits; orbits circular, directed forward; maxillary tomia curving upwards toward midline to form broad, semicircular notch; medial borders of palatine flanges nearly parallel to each other as far back as the opening for internal nares; little or no contact between pterygoids at midline; precondylar fossa lunate; trigeminal foramen facing antero-laterally, situated low on wall of brain case; breadth between postero-lateral corners of palatines equal to 40 per cent of skull length from snout to occipital condyle.

Not only does the British Museum specimen provide new information about parts of the skull that were not preserved in the type, but it also permits an important correction of Swinton's description. The snout region of BMNH—R. 8432 is little damaged and it is possible to determine unequivocally that, contrary to his belief, nasals were lacking, as in all pelomedusids.

The type as preserved is 4½ inches (11.4 centimeters) long according to Swinton. A comparable portion of the British Museum specimen measures 9.3 centimeters in length. The total length of this skull (from snout to occipital condyle) is approximately 10.2 centimeters. With this information it is possible to calculate the total estimated length of the type skull, assuming that there were no significant ontogenetic changes in proportion, as 12.5 centimeters. Such large skulls indicate that adult representatives of *Shweboemys pilgrimi* must have been imposing creatures, roughly equivalent in size to *Podocnemis expansa,* the largest of the living pelomedusid species.

The most persuasive indication that Swinton adduced to support his contention that *Shweboemys* was a pelomedusid is its palatal structure, which resembles that of *Stereogenys* more than that of any other known turtle. This, however, is not a diagnostic character, since it occurs elsewhere within the family only in *Bothremys* and is rather widespread among cryptodires.

For taxonomic purposes, therefore, the most significant additional information provided by the British Museum skull is the evidence that enlarged carotid channels were present (Fig. 1A). Such structures are known only in the pelomedusid genera *Podocnemis* and *Stereogenys* and are not known in any other turtle group. Much more substantial grounds now exist, consequently, to confirm Swinton's belief that *Shweboemys* is truly a pelomedusid.



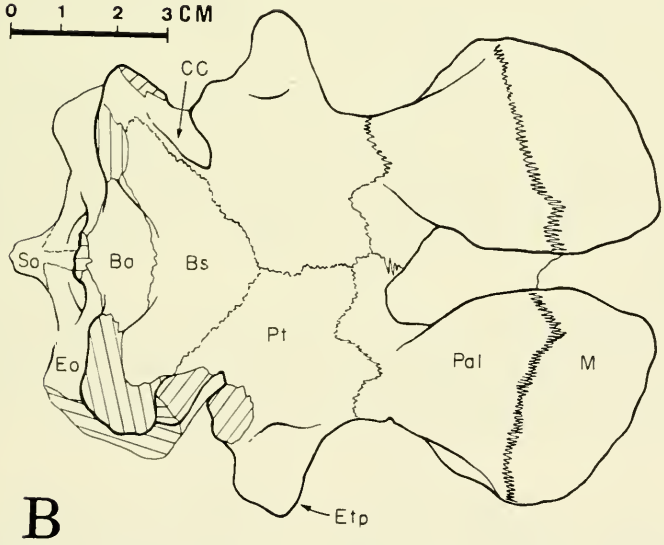


Figure 1. Palatal views of: A—*Shweboemys pilgrimi* (BMNH—R. 8432); B—*Shweboemys gaffneyi* (BMNH—R. 8570). Solid parallel lines represent areas of breakage. Matrix is indicated by randomly arranged V's. Stippled areas cover region in which thin sheets of surface bone have broken off, thus making exact determination of position of sutures difficult. Abbreviations: PM = premaxilla; M = maxilla; Pal = palatine; Pt = pterygoid; Bs = basisphenoid; Bo = basioccipital; Eo = exoccipital; So = supraoccipital; Etp = ectopterygoid process; cc = carotid channel.

There does not appear to be any contact between the pterygoids at the midline, although less than perfect preservation on the ventral surface of the basicranium of BMNH—R. 8432 necessitates consideration of the possibility that these bones may have barely met in an undamaged specimen (see Plate IIA and Fig. 1A). Even if the pterygoids actually did meet at the midline, their junction was clearly not extensive.[1] Among pelomedusids, this particular configuration is found only in this species and its African relative, *Shweboemys antiqua.* Another distinctive character is the position of the foramen for the trigeminal nerve (Plate IIIA), which Swinton (1939: 551) was unable to detect in the type specimen because of poor preservation. Instead of being situated above the floor of the brain case and directed laterally, as in nearly all other pelomedusids, it is positioned much lower and faces antero-laterally. In *Bothremys cooki* this foramen is evidently situated as far down on the side of the brain case as in *Shweboemys pilgrimi,* but it does not seem to have been directed antero-laterally (Gaffney and Zangerl, 1968: 220, figs. 13, 14, and 16).

Breakage of the anterior ends of the premaxillae prevents an exact determination of the shape of the external nares (Fig. 2A). As preserved, the narial opening is ellipical, with its transverse axis the longest. Damage to this same region also leaves some question as to the actual shape of the upper jaw. Conceivably, it may have had a downward curving beak, as in adult specimens of *Pelusios niger,* or have simply been notched, as in many other pelomedusids. Alternatively, its present rounded contour may actually reflect its original shape. Whatever the case, it is clear that there was a strong median indentation of some kind at the midline.

Although the scroll-like outer portion of the laterally projecting ectopterygoid processes have not been preserved in either specimen of *Shweboemys pilgrimi,* these structures did exist. Evidence to this effect is preserved on BMNH—R. 8432, where the basal portion of these protuberances can be seen on both sides.

[1] Contrary to Swinton's statement (1939: 550), no portion of the pterygoids is preserved on the holotype. What he evidently interpreted as the palatine-pterygoid suture appears to be a transverse crack across the ventral surface of the palatines (Plate IA).

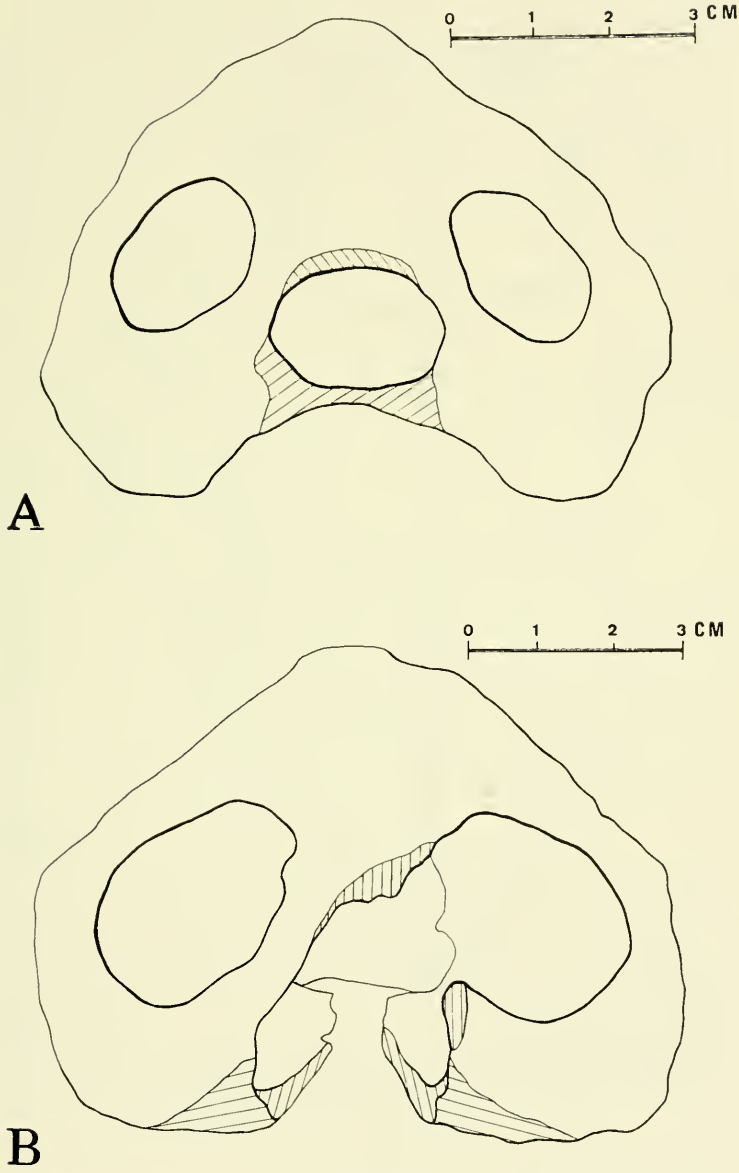


Figure 2. Facial views of: A—*Shweboemys pilgrimi* (BMNH—R. 8432); B—*Shweboemys gaffneyi* (BMNH—R. 8570). Solid parallel lines represent areas of breakage.

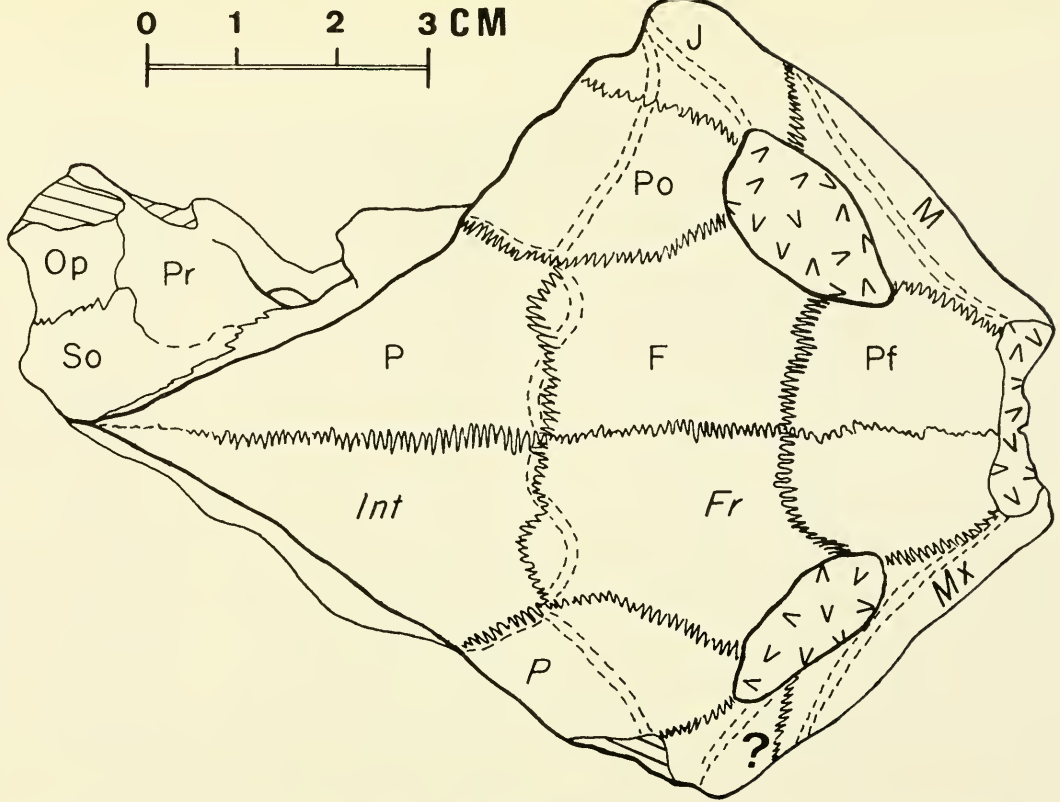


Figure 3. Skull of *Shweboemys pilgrimi* (BMNH—R. 8432) in dorsal view. Parallel dashed lines represent scute sulci. Matrix filling narial aperture and orbits indicated by randomly arranged V's. Solid parallel lines mark broken surfaces. Abbreviations for bones: M = maxilla; Pf = prefrontal; F = frontal; P = parietal; Po = postorbital; J = jugal; So = supraoccipital; Pr = proötic; Op = opisthotic. Abbreviations for scutes: *Mx* = maxillary; *Fr* = frontal; *P* = parietal; *Int* = interparietal; ? = subocular or masseteric.

Scute sulci can be detected on the roof of the British Museum skull (Fig. 3). The anterior border of the interparietal overlapped slightly onto the postero-lateral corners of the frontal bones and was bow-shaped, more like that of *Podocnemis sextuberculata* (*cf.* Siebenrock, 1902, fig. 9) than any other pelomedusid known to me. Behind the orbit a scute intervened between the maxillary and frontal scutes. Whether this was an enlarged masseteric scute, as in *Podocnemis dumeriliana,* or a subocular scute, as in most of the other species of *Podocnemis* (Williams, 1954), is uncertain.

Shweboemys gaffneyi sp. nov.[1]
(Plates IIB, IIIB, IVB)

Type. BMNH—R. 8570, a partial skull lacking the premaxillae, most of the prefrontals, the bones of the cheek region, the quadrates and squamosals, the supraoccipital crest, and whatever supratemporal roofing there may have been.

Hypodigm. The type, only.

Horizon and locality. Early Miocene, Bugti Hills, Baluchistan, West Pakistan.

No locality or stratigraphic data are associated with this specimen, but apparently it was obtained by C. Forster-Cooper during one of his two expeditions to the area around Dera Bugti during the years 1910 and 1911 and would therefore be of the age and from the general region cited above. It was subsequently given to Professor D.M.S. Watson for description, who in turn passed it on to Dr. E. E. Williams for the same purpose. Other commitments having prevented either from formally describing this interesting skull, the task has now fallen to me.

Pilgrim (1908: 144) briefly mentioned that chelonian remains are not uncommon in the Miocene sediments of the Bugti region. Unfortunately, none of these have ever been described. Knowledge of their existence nevertheless reinforces the probability that the skull under consideration is of the age of and from the locality given above.

Diagnosis. Differing from *S. pilgrimi* in: interorbital width less than diameter of orbits; tomial margins of upper jaw (so far as preserved) horizontal, not notched; medial borders of palatine

[1] The species is named for Dr. Eugene Gaffney in recognition of his work on pelomedusid turtles.

flanges curving away from midline; breadth between postero-lateral corners of palatines equal to 50 per cent of skull length from snout to occipital condyle; broad contact between pterygoids at midline; precondylar fossa semicircular; foramen for trigeminal nerve situated relatively higher on ascending wall of brain case and directed laterally. Differing from *S. antiqua* in: lack of forehead groove; orbits round rather than oval; no median notch in upper jaw; broad contact between pterygoids at midline; size much greater.

In total length, this skull is slightly longer than the smaller of the two specimens of *Shweboemys pilgrimi* (10.5 *versus* 10.2 centimeters for the distance from the snout to the occipital condyle). The width at the postero-lateral corners of the palatines is significantly greater, however, indicating that the skull of *S. gaffneyi* was proportionately wider. Compared to *S. pilgrimi,* the orbits of the new species are also proportionately much larger. The increase has been achieved primarily by dorsal emargination of the external face of the maxilla. The diameter of the orbits in *S. pilgrimi* is essentially the same as the distance across the maxilla from the base of the orbit to the tomium. In contrast, the diameter of the orbits in *S. gaffneyi* is nearly twice as great. Because the premaxillae are missing, it is impossible to reconstruct the shape of the upper jaw at the midline. There may have been some kind of median notch, but if so it must have been relatively small and thus quite unlike that of *S. pilgrimi* (see Fig. 2B).

The two Asiatic species differ somewhat in the structure of their secondary palates. In *S. gaffneyi,* the secondary palate is broader than it is long, whereas in *S. pilgrimi* this region is slightly longer than wide (*cf.* Figs. 1A and B). For analyzing proportional differences, direct comparisons may be made between comparable measurements of the two British Museum skulls of *Shweboemys,* each representing one of the Asiatic species, since they are both of nearly the same length and are equally well preserved in the region under consideration. At the point where the sutures between the maxillae and the palatines reach the outermost extent of the secondary palates, the distance across the secondary palate of the type of *S. gaffneyi* is 7.2 centimeters, whereas this same distance in BMNH—R. 8432 is 6.1 centimeters. But the length of this structure is 5.3 centimeters in the former and 6.7 in the latter. Another difference, of unknown biological significance, involves the pitting on the ventral surface of the secondary palate.

In both species, these pits appear to be more abundant on the maxillae than on the palatines. The maxillary pits, however, seem to be deeper, larger in diameter, and fewer in number in *S. gaffneyi* (see Plate II).

No scute sulci are clearly discernible on the preserved part of the skull roof of *S. gaffneyi*. Linear depressions, which might be interpreted as scute furrows, follow the courses of the fronto-parietal and fronto-postorbital bone sutures. But a similar groove running antero-posteriorly along the midline does not have a homologue in any other pelomedusid. Thus I am dubious that any of these indentations necessarily corresponds in position to the actual boundaries between scutes.

The position of the trigeminal nerve foramina and the extent to which the pterygoids meet on the ventral surface of the skull in *S. gaffneyi* are typically pelomedusid and clearly serve to differentiate this species from *S. pilgrimi*, which is specialized in these characters. The skull of *S. gaffneyi* exhibits no features that would bar the species from the ancestry of *S. pilgrimi*.

The skull of *S. gaffneyi* differs from that of *S. antiqua* in a number of respects, of which a few may be mentioned here, pending detailed description of the Fayum species. Size is the most obvious (although not necessarily the most significant taxonomically) difference between the two: the distance from the snout to the occipital condyle in *S. gaffneyi* is more than one and one-half times longer than in *S. antiqua* (10.5 *versus* 6.6 centimeters). The orbits of *S. gaffneyi* are round and directed forward, those of *S. antiqua* are oval and face laterally. There is a forehead groove between the orbits of the latter but not of the former. As in *S. pilgrimi*, and in strong contrast to *S. gaffneyi*, there is little or no contact between the pterygoids at the midline in *S. antiqua*.

DISCUSSION

Of the small number of Asiatic fossil pelomedusids hitherto described, one, *"Podocnemis" indica*, is not well enough known at the present time to merit formal taxonomic assignment. However, *Carteremys* probably was a pelomedusid, and *Shweboemys* certainly was.

The relationships of *Carteremys* within the Pelomedusidae are uncertain. On the basis of skull structure, *Shweboemys* appears to have been more closely related to *Stereogenys* than to any other

pelomedusid. Within the genus, *Shweboemys pilgrimi* may well have been derived more or less directly from *S. gaffneyi*, and there is no reason why this latter species could not in turn have been directly descended from *S. antiqua*. Occurrences of this genus are separated by such great distances and represented by such a paucity of material, however, that future discoveries may reveal that this interpretation is overly simplistic.

Shweboemys is the only pelomedusid genus so far known to have established a successful, enduring lineage outside of Africa or South America. The *Shweboemys* lineage appears to have been restricted to southern Asia and Africa; no pelomedusid has thus far been reported, even questionably, from central or eastern Asia. The localities where the two Asiatic species of this genus occur are very widely separated geographically and no representative has been recorded from the intervening (and considerably younger) Siwalik deposits of India. Nothing, however, has been published on Siwalik fossil turtles for more than three-quarters of a century. Those described by Lydekker (1885), apart from the large testudinids, show relationships to the recent turtle fauna of India, but available collections need to be examined thoroughly with an eye to the possible presence of pelomedusid remains.

Some inferences are possible concerning the ecology of the two Asiatic species of *Shweboemys*: the Irrawaddy beds are fluviatile in origin (Krishnan, 1960: 498), so that this species was evidently not a marine form.[1] In view of the fact that all pelomedusids (except for one or possibly two undescribed fossil genera from Africa) are aquatic, *S. pilgrimi* was probably a freshwater rather than a terrestrial turtle. Pilgrim (1908: 159) referred to the Bugti beds from which *S. gaffneyi* was presumably recovered as a "freshwater formation" and Krishnan (1960: 492) regarded them as being fluviatile, so that this species was in all likelihood also a freshwater rather than a marine form. Moreover, the specialized palatal structures of these two species have definite implications regarding their feeding habits. Like some living trionychids with enlarged secondary palates, their diet may have consisted largely or perhaps even exclusively of molluscs of one sort or another.

[1] I am suggesting elsewhere that the pelomedusids were of marine origin.

ACKNOWLEDGMENTS

I am particularly grateful to Mr. C. A. Walker of the British Museum (Natural History) for bringing to my attention the skull of *Shweboemys pilgrimi* belonging to that institution. To the authorities of the British Museum (Natural History) I am indebted for permission to describe this specimen as well as the type of *S. gaffneyi*. I am also much obliged to Professor Bryan Patterson and Dr. E. E. Williams for critically reading this manuscript, to Professor B. Kummel for help concerning the stratigraphy of West Pakistan and Burma, and to Mr. A. D. Lewis for his skillful preparation work on both of the British Museum skulls. The photographs of the type of *S. pilgrimi* reproduced in Plate I were sent to Dr. E. E. Williams by the authorities of the Geological Survey of India. The figures were drawn by Mr. Laszlo Meszoly. Finally, I would like to express my appreciation to the National Geographic Society for their generous financial support of my research on pelomedusid turtles.

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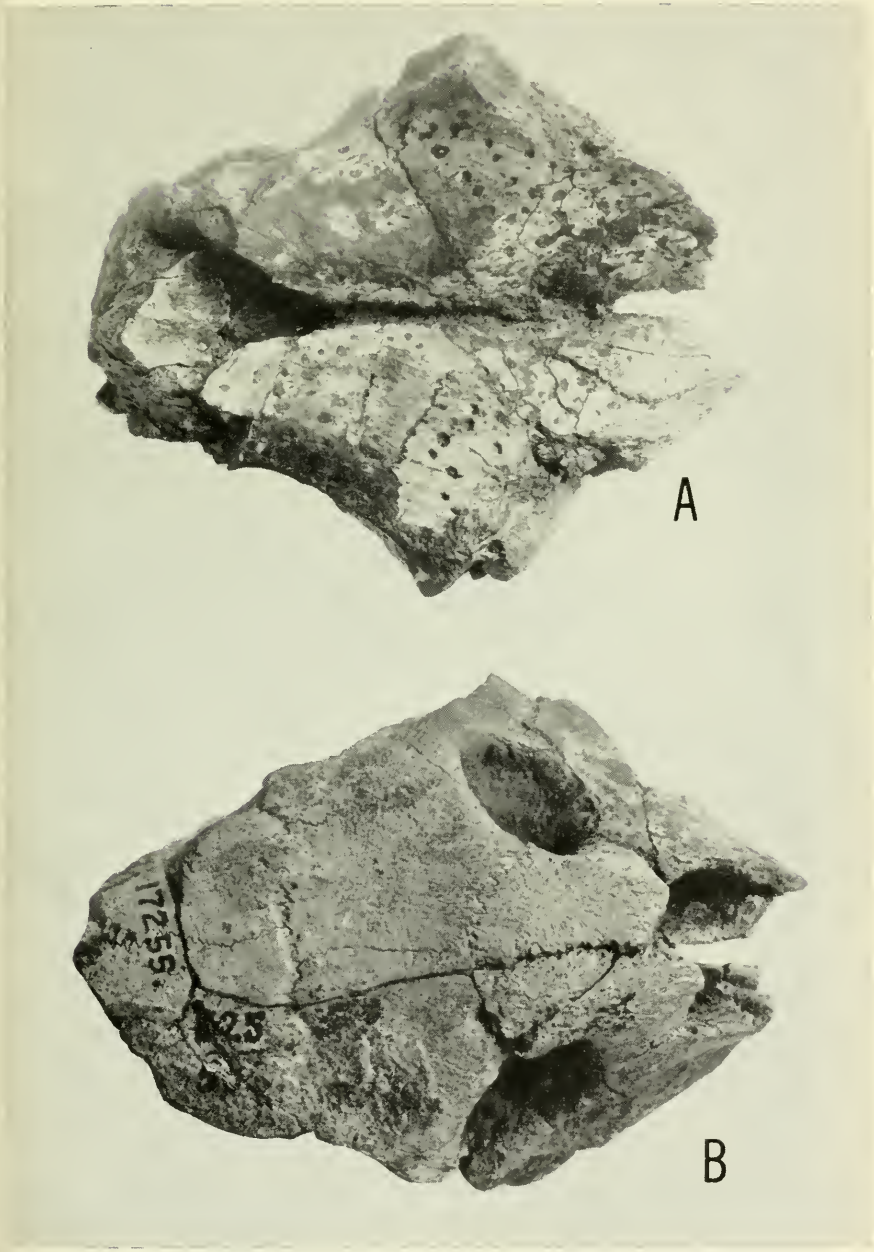
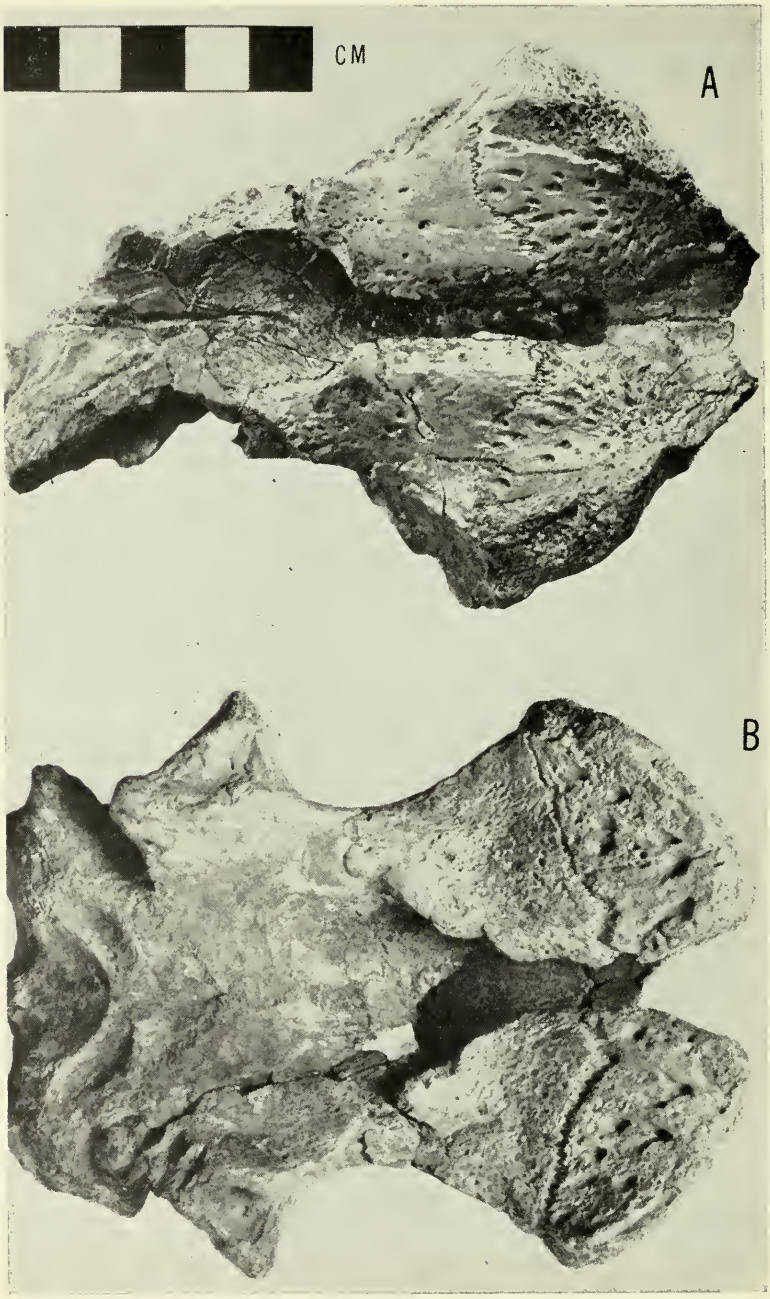
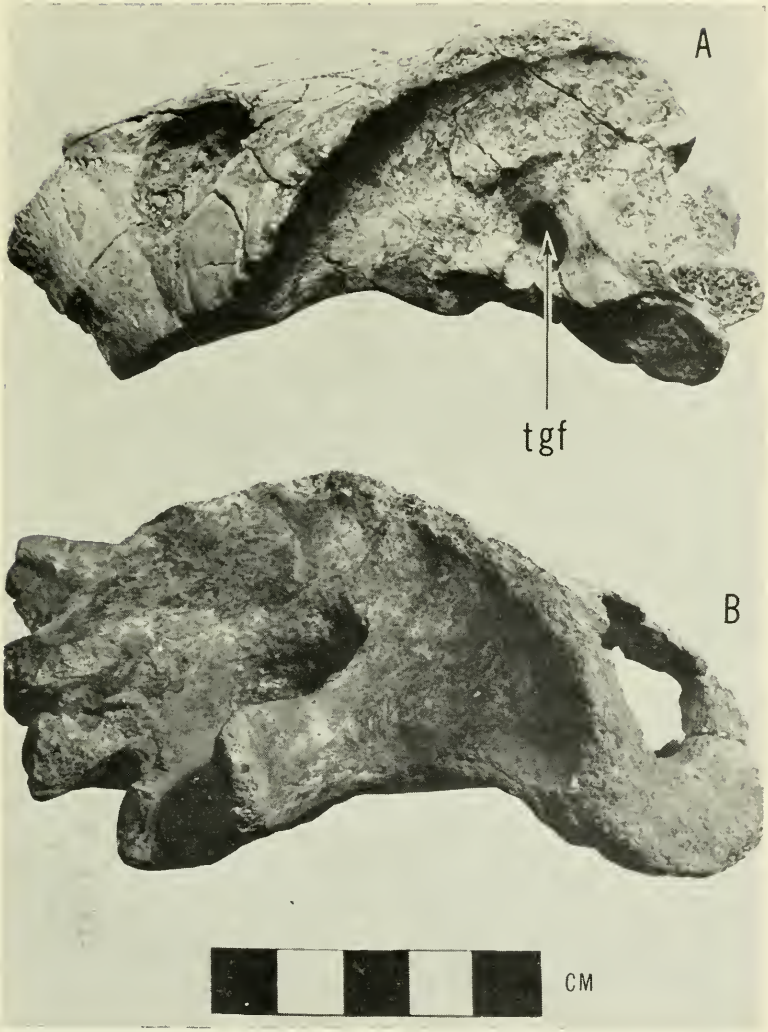


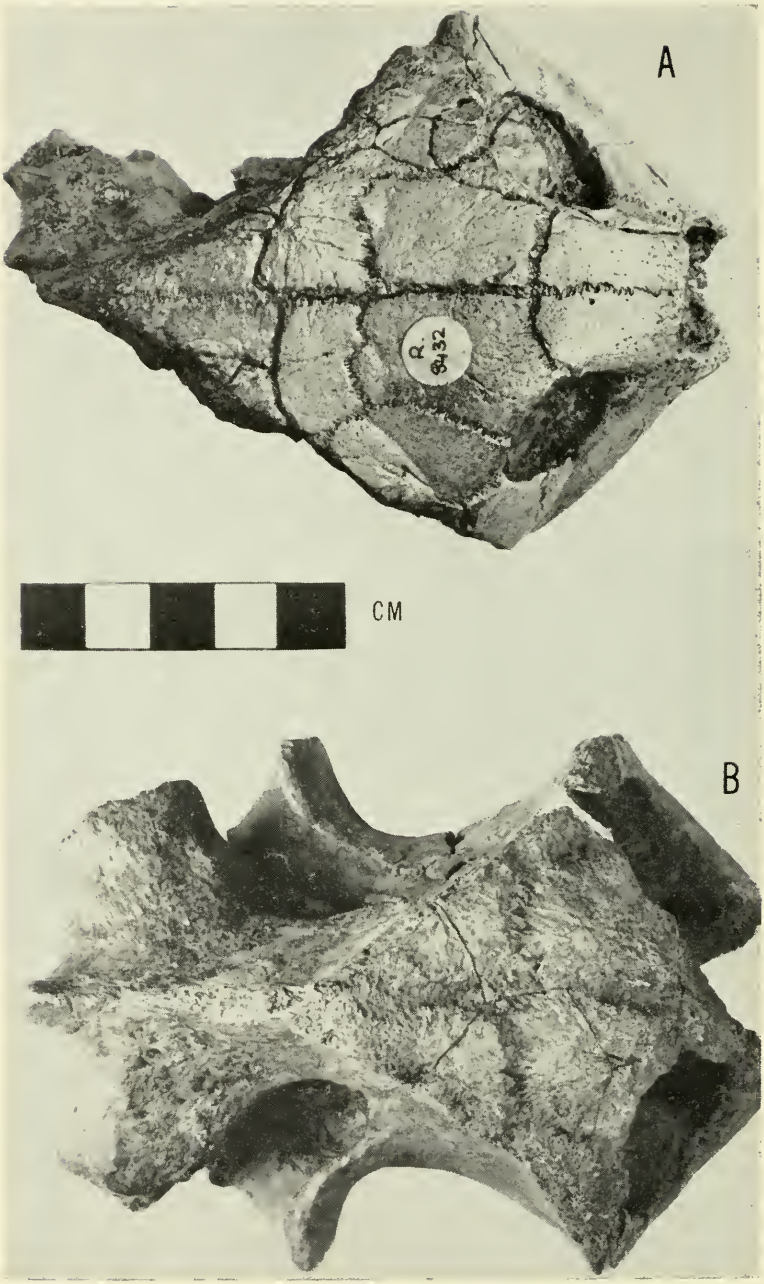
1. Type specimen of *Shweboemys pilgrimi* (GSI 17255): A—palatal view of skull; B—dorsal view. Approximately ¾ natural size.



II. Palatal views of: A—*Shweboemys pilgrimi* (BMNH—R. 8432); B—*Shweboemys gaffneyi* (BMNH—R. 8570).



III. Lateral views of: A—*Shweboemys pilgrimi* (BMNH—R. 8432); B—*Shweboemys gaffneyi* (BMNH—R. 8570). tgf = trigeminal nerve foramen.



IV. Dorsal views of: A—*Shweboemys pilgrimi* (BMNH—R. 8432); B—*Shweboemys gaffneyi* (BMNH—R. 8570).

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. 30 NOVEMBER, 1970 NUMBER 358

South American anoles: *Anolis apollinaris* Boulenger 1919, a relative of *A. biporcatus* Wiegmann (Sauria, Iguanidae)

Ernest E. Williams

ABSTRACT. *Anolis apollinaris* is a central Andean derivative of *A. biporcatus,* probably from an earlier invasion of South America than that which has provided the present Colombian, Ecuadorian, and western Venezuelan populations of the latter species.

Anolis apollinaris Boulenger 1919 was described from a unique type, a female, said to come from "near Bogota." The description made no mention of relationships.

The next mention of the species was made by Burt and Burt (1931: 255), who referred numerous Colombian specimens in the American Museum to this species. They suggested that the species belonged to the *"chrysolepis* stock" but also said that their specimens closely resembled *A. gemmosus* of Ecuador with which they believed *A. apollinaris* "may prove to be identical or subspecifically allied." An examination of the type of *apollinaris* in the British Museum shows that these statements of relationships are entirely mistaken and that the specimens referred to the species by Burt and Burt—one specimen received in exchange from the American Museum by the Museum of Comparative Zoology—are misidentified.[1]

[1] The type of *A. gemmosus* O'Shaughnessy has also been examined. It is not of *chrysolepis* stock nor related at all closely to the two species misidentified by Burt and Burt as *A. apollinaris.* The affinities of *A. gemmosus* are with *A. fasciatus* Boulenger and *A. andianus* Boulenger.

A correct judgment on the affinities of *A. apollinaris* was made by E. R. Dunn in 1944 (p. 25), who at that time reported:

"The Instituto de La Salle has a specimen of this lizard (described from 'near Bogota') from Paime, Cundinamarca, 1038 meters. A number of students have overlooked the statement that this is a large *Anolis* (type head-body length 106 mm) and misapplied the name. Thus the "*Anolis apollinaris*" of Burt and Burt (1921 [sic], p. 255) is not Boulenger's species but a composite of two smaller species, *incompertus* Barbour from Villavicencio and *mariarum* Barbour from Medellin[1]. True *apollinaris* is allied to *solifer* of Santa Marta and *copei* of Central America."

The two latter names are now regarded as synonyms of *biporcatus* (see Williams, 1966) and it is with this species, which ranges from Mexico to Ecuador, that *apollinaris* requires comparison.

Brother Niceforo Maria of the Instituto La Salle tells me that Dunn's specimen of *A. apollinaris* was one of many specimens destroyed in a fire at the Institute in 1948. Fortunately, a number of previously unreported specimens have been discovered, one in the Institut Royale (Brussels), a series in the Zoologische Staatsammlung (Munich) and three, indeed, in more recent collections of the Instituto La Salle (ILS), and two more in the American Museum of Natural History (AMNH).

On the basis of these new specimens and the type specimen at the British Museum (BM), I present a revised standard description of the species:

Anolis apollinaris Boulenger

Type. BMNH 1919.3.6.7 (1946.8-13.22), from near Bogotá, Cundinamarca, Colombia.

Referred specimens. (All Colombia.) *Antioquía* (all Cauca Valley): AMNH 38725, Sabanalarga; ILS 81, Puerto Antioquia. *Caldas*: ILS 101, Pueblo Rico. *Cundinamarca*: Brussels 3580, La Esperanza, 1250 m; ILS 65, Paime; ILS 106, Quipile; Munich 427-432, San Pablo, west side of cordillera between Bogotá and La Dorada. "Western Colombia": AMNH 4844.

[1] *A. incompertus* Barbour is a composite species: specimens from Villavicencio are *A. chrysolepis scypheus* Cope and, from near Bogota, *A. tropidogaster* Hallowell. *A. mariarum* Barbour is a synonym of *A. antonii* Boulenger. All types have been examined.

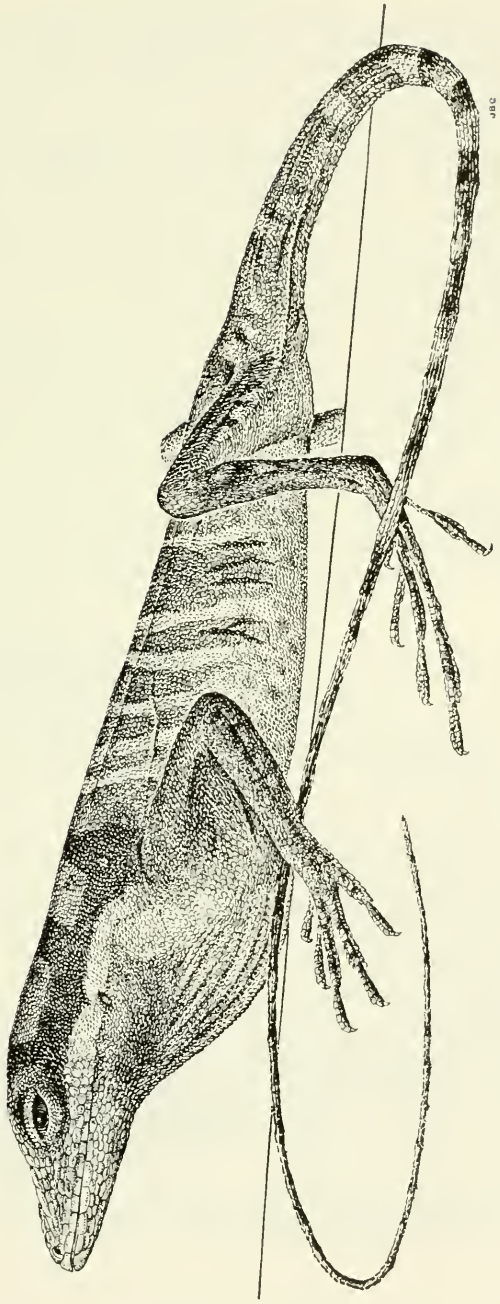


Figure 1. *Anolis apollinaris* Munich male, No. 423. Lateral view.

Diagnosis. Allied to *biporcatus* Wiegmann and its subspecies *parvauritus* Williams but differing in color, in one or no scales separating nasal from rostral, and in a modally higher number of lamellae under phalanges ii and iii of the fourth toe.

Head. Head scales small, sharply uni- or tricarinate. Ten to thirteen scales across snout between second canthals. A distinct frontal depression, scales within it not smaller than surrounding scales. Five to nine scales border rostral posteriorly. Circumnasal scale separated from rostral by one small scale or in contact. Six to seven scales between circumnasals dorsally.

Supraorbital semicircles separated from each other by 2–4 scales, from the supraocular disk by one row of smaller scales. Supraocular disk not very distinct, of 4–12 keeled scales grading laterally into granules. One to three overlapping elongate supraciliary scales, continued posteriorly by granules. Anterior corner of supraocular filled by larger subgranular scales. Canthus sharp, of 6–7 overlapping scales, the first and second or second and third the largest. Five to seven loreal rows, subequal or the uppermost largest. Temporal scales granular. A distinct double line of enlarged intertemporal scales. Supratemporals granular, slightly smaller than

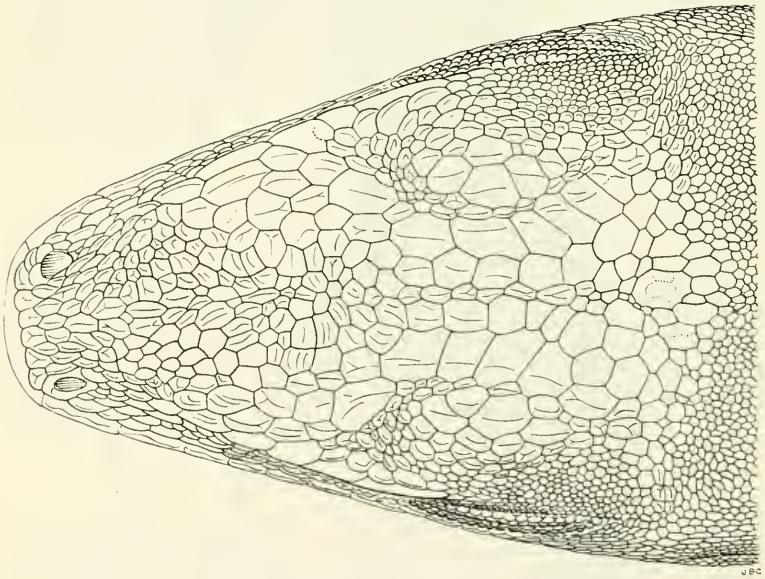


Figure 2. *Anolis apollinaris* Munich No. 422. Dorsal view of head.

temporals. Scales surrounding interparietal moderately to abruptly enlarged, swollen, largest anteriorly and laterally. Interparietal less than or greater than ear, separated from semicircles by 3–4 scales on each side.

Suboculars separated from supralabials by one row of scales (or narrowly in contact), anteriorly separated from canthal ridge by one scale, posteriorly continued by an indistinct double row of smaller scales. Seven to eight supralabials to center of eye.

Mental slightly wider than long, in contact with 4–8 scales between supralabials posteriorly. Sublabials not well differentiated. Central throat scales quadrangular, swollen, gradually increasing in size laterally.

Dewlap. Dewlap in male large with close-packed scales. A gular fold only in female, moderate, scales rather closely packed.

Trunk. Middorsals slightly enlarged, swollen, keeled. Dorsal and flank scales keeled, subequal. Ventrals larger, weakly keeled, imbricate, *not mucronate.*

Limbs. Largest fore and hind limb scales strongly unicarinate, except at knee and elbow, smaller than largest ventrals. Supradigital scales multicarinate. Twenty-four to twenty-seven lamellae under phalanges ii and iii of fourth toe.

Tail. Slightly compressed, almost evenly scaled all round. Verticils indistinct. All scales keeled. Enlarged postanals in male.

Size. Type: 106 mm snout-vent length.

Comparison. Table 1 lists the major features differentiating *A. apollinaris* and *A. biporcatus.* I comment on each of these features below:

1. *Scales in narial area.* The exact pattern of the scales surrounding the naris and their relation to the rostral have been repeatedly used in lizards generally (e.g., geckos), and this pattern has also proved empirically very useful at the species level in *Anolis.* Published examples of the utility of this character at the species level are Ruibal and Williams (1961) and Lazell (1964). Although, like all squamation characters in *Anolis,* these patterns are subject to some intraspecies variation, they are rather surprisingly constant. Frequently a single pattern is consistently maintained; this is usually a simple one. More complex patterns tend to greater variation but the variations are readily derivable from the modal condition (Fig. 3). The pattern of *apollinaris* is always simpler than that of *biporcatus* and may be more primitive. (The judgment that this pattern may be more primitive is based not upon

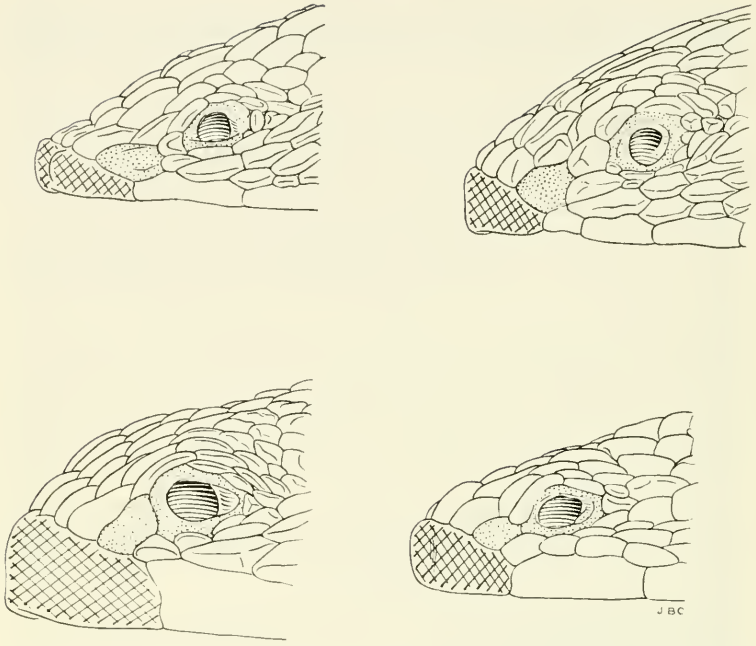


Figure 3. Nasal rostral relationships. Upper left: *Anolis biporcatus biporcatus,* MCZ 15426. Upper right: *A. b. parvauritus,* MCZ 78942. Lower left: *A. apollinaris,* Munich 422. Lower right: *A. fraseri, MCZ* 43772.

its simplicity but upon its association with other characters regarded as primitive and on its occurrence in species regarded on other grounds as primitive.) The variation in *apollinaris* is in the direction of the pattern in *biporcatus,* but there is no overlap. This is a sharp and clear distinction.

2. *Supraciliary scales* (Fig. 4). Again the pattern of this area tends to be species specific and again the condition in *apollinaris* tends to be simpler and perhaps more primitive than that of *biporcatus.* The common pattern in *biporcatus* is indeed unusual (though not unique). Two patterns are common for the supraciliary region of anoles: (1) one or more elongate supraciliaries followed by undifferentiated granules; (2) one or more elongate supraciliaries followed by a double series of enlarged scales rather even in size.

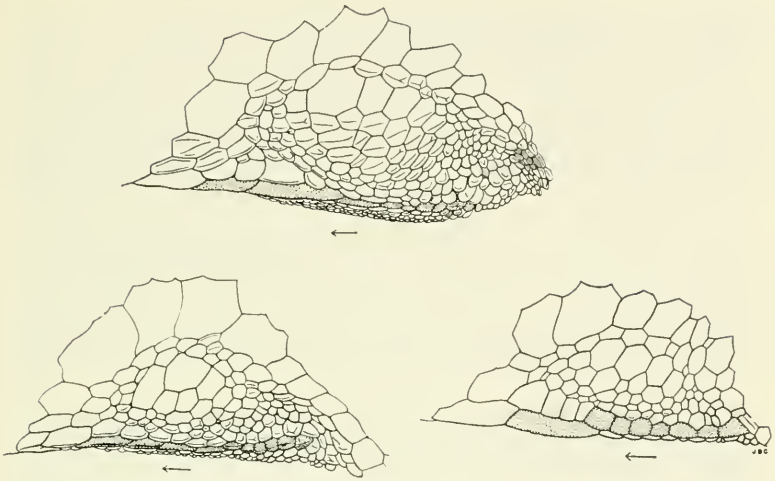


Figure 4. Supraciliary area. Top: *Anolis apollinaris,* Munich 422. Lower left: *A. b. biporcatus,* MCZ 15426. Lower right: *A. fraseri,* MCZ 43772.

A. biporcatus, exhibiting several rather short supraciliaries grading into large scales that tend to grade again into granules, presents a condition hardly more frequent than that of *A. fraseri* with its series of quadrate scales along the whole supraciliary margin, the first of these sometimes elongate.

3. *Scales around interparietal.* In general, the degree of enlargement of scales around the interparietal is a good specific character in *Anolis.* Particularly valuable may be the degree of enlargement of the scales posterior to the interparietal as compared with the adjacent dorsal or supratemporal scales. There may be rapid intergradation of enlarged scales lateral to the interparietal into much smaller dorsal and supratemporal scales, or the scales behind the interparietal may be sharply and conspicuously larger than dorsal or supratemporal scales (as in some *apollinaris*). The two subspecies of *A. biporcatus* differ in this regard. *A. apollinaris* is variable; perhaps the variation is geographic, but there is not enough material to say.

4. *Ear shape and position.* The ear of *apollinaris* is quite different from that of either southern or northern *biporcatus.* It is

closer in size to that of southern *biporcatus* but quite distinct in its obliquity, a rather unusual feature.

5. *Ventral keeling.* This character is minor. Keeled ventrals may be a good species character, but there are many instances of intraspecies variability, both geographic and (typically qualitatively less extreme) at a single locality. *A. apollinaris* has the ventrals more weakly keeled than either subspecies of *biporcatus.*

6. *Toe lamellae.* The number of toe lamellae is an extremely useful character in *Anolis* and very characteristic of species. It is, however, subject to variability (a range of 6 or 7 is quite usual) and overlap is, as in the present case, frequent. *A. apollinaris* tends to a higher number of toe lamellae than either subspecies of *biporcatus.*

7. *Color.* I have no descriptions of color in life of *apollinaris* and the varying colors of *biporcatus* as preserved (it is uniform green in life) do not make comparison very easy. Boulenger described the type female as "Dark olive above and on the sides, with a fine blackish network, head and a vertebral band pale, the latter with narrow transverse processes; small round light spots on the sides and tail; forearm, tibia and lower parts pale green."

The Brussels specimen has preserved its pattern rather well. Description follows: Head greyish. A dark streak from back of eye to shoulder, there merging with dark flanks. Below this, labials and nape lighter, their color continuous with the smudged grey of the throat. A light brown middorsal zone, irregularly darker laterally, bordered on each side by a narrow grey line. Flanks dark brown with indications of white spots or broken narrow vertical white bars. Forelimbs obscurely annulate, hind limbs boldly so. Tail above with longitudinally oval light spots with irregularly dark centers. Belly lighter than any part of dorsum but still heavily infuscated. Tail below lighter still.

The new specimens resemble the Brussels specimen in head coloration, as the British Museum type now does; presumably the latter differs from Boulenger's description as a result of change during preservation.

A. apollinaris, when compared with *A. biporcatus,* differs in few and superficially trivial ways. The ventrals are less strongly keeled. There are fewer scales between nostril and rostral: one or more rather than two or three. The color is quite unlike anything I have seen in *biporcatus.* I am neither confident that this form is a full

species nor convinced that it is not. It is certainly not to be confused with Mexican or Central American *biporcatus,* nor with the south Colombian-Ecuadorian population, nor does it resemble the two Venezuelan specimens of that species. Whether it is distinct from, or intergrades with, some of the other Colombian or the Ecuadorian populations is a matter for future discovery. Provisionally, since it was described as a species, it may remain so allocated.

A. biporcatus has the distribution of a recent immigrant into South America, extending from Panama through the Choco region of Colombia down into Ecuador west of the Andes and extending eastward through the Santa Marta Mountains into western Venezuela. *A. apollinaris,* now recorded from Antioquia, Caldas, and Cundinamarca, may be supposed to have arisen from *A. biporcatus* by isolation and subsequent minor modification in the central Andean regions of Colombia. Since it has some primitive features (e.g., nasal-rostral relationship) and since it has reached species status, it may represent an earlier invasion of South America than that which resulted in *A. b. parvauritus* Williams and the Venezuelan specimens of *A. b. biporcatus.*

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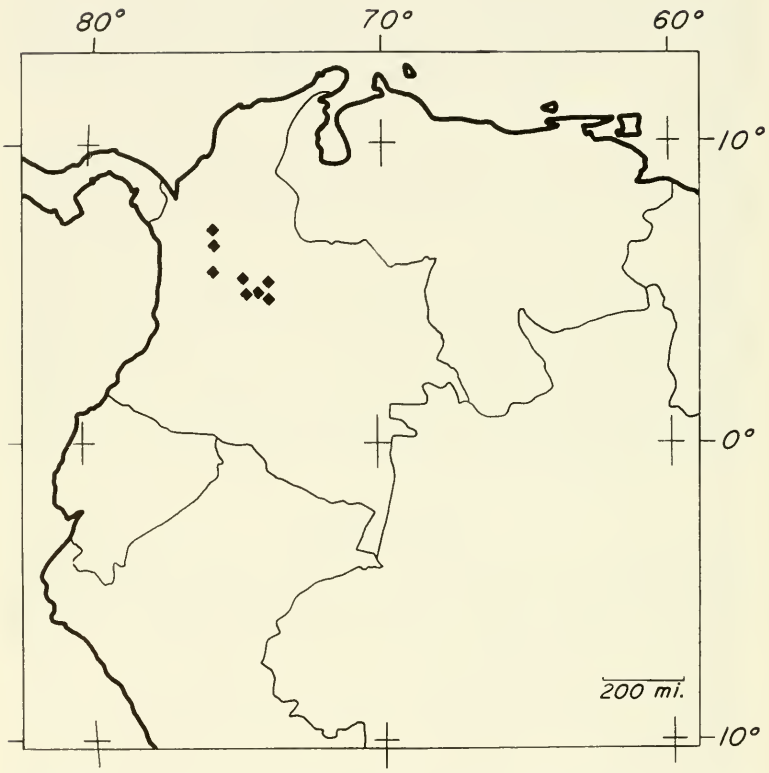

Figure 5. Map of the distribution of *Anolis apollinaris* in central Colombia.

TABLE 1

	apollinaris	*b. biporcatus*	*b. parvauritus*
scales across snout	9-13	7-11	8-13
scales between nasal and rostral	0-1	2-3	2-3
scales between supra-orbital semicircles	2-4	1-4	0-3
supraciliaries	1-2 elongate plus series of small scales of rather uniform size	usually 3-4 short supraciliaries plus a series of small scales of variable size	as in *biporcatus*
scales behind interparietal	variable, slightly to abruptly larger than dorsals	abruptly larger than dorsals	grading gradually into dorsals
scales separating interparietal from semicircles	3-5	3-6	3-7
loreal rows	5-8	5-10	6-9
supralabials to center of eye	7-8	8-11	7-12
ear	small to moderate	moderate to large, vertical	small
ventrals	weakly keeled	strongly keeled, mucronate	strongly keeled, mucronate
lamaellae under phalanges ii and iii of fourth toe	25-27	22-26	22-26

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. 30 NOVEMBER, 1970 NUMBER 359

The Swimbladder as a Juvenile Organ in Stromateoid Fishes

Michael H. Horn[1]

ABSTRACT. The swimbladder regresses in 14 of the 15 genera of stromateoid fishes and apparently in each case before maturity is reached. In one genus the swimbladder is absent. The organ appears to be completely functional and is present in juvenile fishes that inhabit the surface layers of the ocean, often in association with jellyfish medusae or floating objects. In the transition from the juvenile to the adult habitat and mode of life, the swimbladder regresses to a nonfunctional state, and other morphological changes occur.

A detailed study in progress of the state and structure of the swimbladder in stromateoid fishes in relation to their evolution and ecology shows that the organ regresses with age in 14 of the 15 genera comprising this suborder of perciform teleosts. The regression of the swimbladder occurs at different ages, depending upon the species in question and seems to be correlated with other morphological changes and with certain changes in mode of life. Thus, the state of the swimbladder may be useful in predicting or determining at what age or size a particular species undergoes a shift in habitat or way of life.

The suborder Stromateoidei consists of six families (Haedrich & Horn, 1969), the members of which range in maximum size from about 30 to about 120 centimeters. It is a fairly diverse group of temperate and tropical marine fishes, which, as adults, variously occupy a wide range of depths in coastal and oceanic waters. The Stromateidae occur at all depths over the continental shelf. The Ariommidae are benthic or benthopelagic on the shelf.

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The Centrolophidae are either coastal, as in *Hyperoglyphe* and *Seriolella,* or oceanic at various depths, as in *Centrolophus* and *Icichthys.* The Nomeidae, Tetragonuridae, and Amarsipidae are oceanic usually in epi- or mesopelagic layers. However, as occurs in many other marine fishes, the larvae and juveniles of stromateoids are pelagic in the surface layers, mostly in the upper 100 meters.

Stromateoid fishes commonly undergo marked changes when approaching maturity, and these changes are often associated with the migration from the surface layers to the deeper layers where the fishes live as adults (Haedrich, 1969). Along with certain changes in body proportions (see Haedrich, 1967; and Horn, 1970), including, frequently, changes in the length of paired fins, the swimbladder regresses. This regression and the significance of the swimbladder in the life of young fishes are discussed below.

MATERIALS AND METHODS

Specimens examined are from the collections of the British Museum (Natural History); the Zoological Museum, Copenhagen; and, the Woods Hole Oceanographic Institution. The fishes from the last institution will ultimately be deposited in the Museum of Comparative Zoology, Harvard University. Specimen data will be included in a forthcoming comprehensive paper on stromateoid swimbladders.

Swimbladder volumes were calculated treating the bladder as an ellipsoid. Body volumes were determined by displacement in water. Ten per cent was allowed for shrinkage of the preserved material, and volume determinations were made from swimbladders that were in most cases well expanded. The number of retial capillaries was estimated from thin sections of swimbladders.

RESULTS AND DISCUSSION

Very little mention has been made of the swimbladder in stromateoids. Jordan & Evermann (1896) stated that the organ was "usually absent" in the Stromateidae. Fowler (1936) indicated that it was "present or absent" in his treatment of several stromateoid genera. Grey (1955) reported it to be absent in *Tetragonurus.* Haedrich (1967) cited its presence in *Arionmma.* While I have not yet examined every species, I have found a swimbladder to be present in all genera except *Pampus.*

The swimbladder in stromateoids (Fig. 1) is euphysoclystous, i.e., with a distinct gas-resorbing area—a posterior chamber separated from the anterior by a diaphragm—and has unipolar retia that are either medial or posterior in position. It is generally of a relatively simple type found in a number of perciform fishes (N. B. Marshall, personal communication).

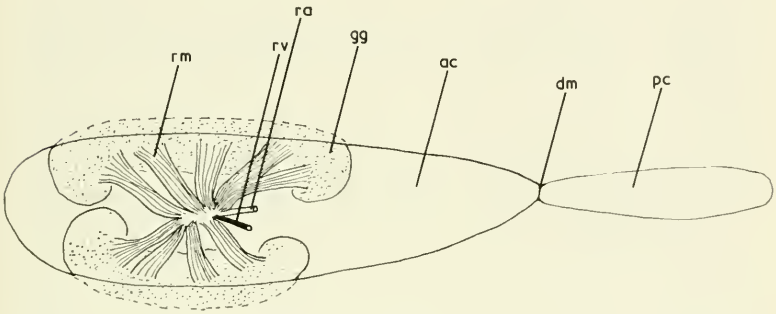

Figure 1. Ventral (slightly flattened) view of the swimbladder of *Nomeus gronovii,* 26.4 mm SL; rm = rete mirabile; rv = retial vein; ra = retial artery; gg = gas gland; ac = anterior chamber; dm = diaphragm; pc = posterior chamber. (× 33)

The swimbladder in these fishes is relatively small and frequently below the 3.1–5.7 range of percentage volumes calculated by Alexander (1966) to be necessary for neutral buoyancy in sea water (Table 1). Measurements of swimbladder percentage volume for *Hyperoglyphe, Cubiceps,* and *Ariomma* show the organ to be within the above range, but in other genera, notably *Schedophilus* and *Nomeus,* the percentage volume may be as low as 0.5 or 0.6 per cent. Some calculated values may be lower than normal because of the swimbladder being in a slightly contracted state. The organ does appear to be completely developed and almost certainly functional. The blood supply is complete, and the surface area of the gas gland and the length of the retia in relation to swimbladder size (Table 1) compare closely with the range of values calculated by Marshall (1960: tables 3, 4, & 5) for deep-sea fishes with well-developed swimbladders. The organ is fully formed in the smallest individuals (9 mm SL) that have been examined. Regression to a nonfunctional state occurs, apparently in all species, before maturity is reached.

TABLE 1.

Swimbladder measurements and ratios of some stromateoid fishes. Either single* or mean values are listed.

Family and Species	*Size Range of fish mm SL*	*Percentage Volume of Swimbladder %*	*Surface Area of Gas Gland/ Swimbladder Volume*	*Length × Width of Swimbladder/ Surface Area of Gas Gland*	*Length × Width of Swimbladder/ Retial Length*	*Total Retial Capillary Length/ Swimbladder Volume*
Centrolophidae						
Schedophilus medusophagus	10.4-30.1	0.8		1.1	1.2	
Icichthys lockingtoni	16.3	2.7	1.2*	1.4*	2.1*	
Hyperoglyphe perciforma	23.4-47.7	4.3	0.2	3.4	12.5	65
Stromateidae						
Peprilus triacanthus	12.0-40.2	2.7	0.3*	3.0	13.4	160*
Nomeidae						
Psenes cyanophrys	9.1-60.8	2.8	0.4	3.9	50.0	
Nomeus gronovii	11.6-33.8	1.0	0.4	4.1	13.6	
Cubiceps gracilis	16.5-30.5	3.9	0.4*	2.5	9.0	215
Tetragonuridae						
Tetragonurus cuvieri	26.0-54.3	2.0	0.1*	4.5	3.7	
Ariommidae						
Ariomma sp.	16.5-30.7	3.5	0.5	4.4	8.7	270
Amarsipidae						
Amarsipus carlsbergi	22.0-67.5			2.4	4.3	

Being fully developed and certainly capable of hydrostatic adjustment, the stromateoid swimbladder seems very unlikely to be merely an evolutionary remnant. The clue to its significance appears to lie in the behavior of the juveniles. The young of all or nearly all of the species live in the surface layers and frequently in association with jellyfish medusae or other animate or inanimate floating objects. Protection is presumably provided by the medusae or floating objects, and the fishes feed upon the small invertebrates concentrated around the objects or upon the jellyfishes themselves. This existence seems to require both considerable maneuverability and the ability to hover and remain motionless in midwater. I have observed young *Peprilus triacanthus* hovering beneath and near the tentacles of the sea nettle, *Chrysaora quinquecirrha,* and they show little locomotor activity except for backing of water by the pectoral fins. Mansueti (1963) has made similar observations on *Peprilus alepidotus* (= *P. paru.*). Few, if any, of the stromateoid genera which consort with medusae are completely immune to jellyfish toxins but merely avoid the tentacles, according to observations made by Mansueti (1963) on *P. alepidotus,* by Maul (1964) on *Mupus* (=*Schedophilus*), and myself on *P. triacanthus.* Lane (1960) reports that *Nomeus gronovii* can survive doses of *Physalia* toxin as much as ten times that which would kill other fishes of the same general size and type; however, *Nomeus* still exhibits considerable agility in avoiding the tentacles of *Physalia.*

The swimbladder, even if small, would provide a degree of buoyancy, although not necessarily complete neutral buoyancy. During the period of life in which the fishes have a gas bladder, the skeleton is not well ossified and the musculature may not be completely developed; thus, the juveniles probably have a lower specific gravity than the adults. In those adults with soft musculature and light ossification, such as *Schedophilus,* the swimbladder probably becomes unimportant and uneconomical because of a change in mode of life, even though, as in juveniles, a small volume of gas would provide nearly neutral buoyancy. Using Alexander's (1966) formula for calculating the percentage swimbladder volume necessary to achieve hydrostatic equilibrium, I find that only a 1 per cent reduction in specific gravity of the fish lowers the required percentage volume from 3.1 per cent, the lower figure in Alexander's calculated range, to 2.2 per cent. The latter figure is within or near the range of volumes for most of the stromateoid

genera (Table 1). Also, the more firmly muscled and more heavily ossified fishes, such as *Hyperoglyphe,* have greater swimbladder volumes than those with softer muscles and lighter bones, such as *Schedophilus* (Table 1). An exception is *Nomeus,* which has relatively firm musculature but a small swimbladder.

The regression of the swimbladder is a gradual process, with the sac diminishing and the gas gland becoming a small yellowish mass before being completely resorbed. The mass representing the regressed gas gland may persist in the mesentery beneath the kidney for a considerable period of time after the swimbladder becomes nonfunctional. In none of the stromateoids does the swimbladder appear to become fat-filled upon regression as it does in some deep-sea fishes (Marshall, 1960).

It is meaningful to consider the duration that the swimbladder remains functional in the different stromateoid genera in relation to the time of change in habitat and mode of life. *Nomeus* among the stromateoids appears to have the most intimate and enduring association with jellyfishes, usually with the siphonophore, *Physalia.* The fish may remain with *Physalia* throughout its life, although this is uncertain. Significantly, *Nomeus* retains what seems to be a functional swimbladder longer than any other stromateoid that has been examined. The largest specimen I have studied (142.7 mm SL) had a relatively large sac with a somewhat contracted gas gland and was captured at the surface with *Physalia.* It has not been possible to determine whether or not the large specimens that have been found with *Physalia* were mature.

The swimbladder of *Peprilus triacanthus* is usually completely regressed by the time the fish reaches a length of 100 mm SL, and this is about the size at which it has completely abandoned jellyfish medusae. Large individuals ($>$ 100 mm SL) of *P. triacanthus* do not hover as do the juveniles but swim continuously. The pectoral fins increase in relative length with age and are used more extensively for propulsion in adults than in juveniles. The angle through which the pectorals are adducted apparently provides lift. (The locomotion and buoyancy of *P. triacanthus* are being considered in a separate study.) Continuous swimming with some degree of pectoral propulsion is probably the rule in adult stromateoids.

In *Stromateus fiatola,* the swimbladder is greatly regressed at a fish length of 75 mm SL, a size at which the fish seems to have

ended its association with medusae (Mansueti, 1963: 60). In the size interval of 75 to 100 mm SL, this species loses the pelvic fins, and its coloration changes from a vertically-banded pattern to a more uniform one in which there are often dorsal spots.

Tetragonurus is a strictly oceanic genus (Grey, 1955), and its swimbladder is considerably regressed when the fish reaches a size of 50 mm SL. The young have been found associated with medusae in the surface waters (Mansueti, 1963: 60). According to Haedrich (1967), the adults are probably members of the meso- or bathypelagic fauna.

Finally, *Pampus,* a coastal genus and the one considered by Haedrich (1967) to be the most advanced of the stromateids, evidently has no swimbladder. Whether fishes of this genus associate with medusae as frequently as other stromateids is not known. There are indications that they do not. According to Suyehiro (1942), *P. argenteus* does feed to a certain extent on jellyfishes in Japanese waters. However, studies by Kuthalingam (1963) and Nath (1966) show that both juveniles and adults of this species off the Indian coast are macroplankton feeders whose diet largely depends upon seasonal changes in abundance of crustaceans and polychaetes; this may indicate that the young do not regularly associate with medusae. Also, the pectoral fins of *Pampus* become quite long early in life and do not greatly increase in relative length with age as they do in *Peprilus,* another stromateid, and certain other genera. At a fish size of 30 mm SL, the pectoral length of *Pampus argenteus* is about 40 per cent of the standard length compared to only about 30 per cent in *Peprilus paru,* which has a very similar body shape. The pectoral length in *Peprilus triacanthus* of the same size is about 25 per cent of standard length. The relative length of the pectorals has increased to 40 per cent in *P. paru* and to about 35 per cent in *P. triacanthus* at a size of 80 mm SL. Thus, assuming that hovering beneath objects and possession of a swimbladder are related and that increased pectoral length is important in continuous swimming, it seems that members of the genus *Pampus* acquire the adult mode of locomotion and habit at an earlier stage than most other stromateoids and, in so doing, completely dispense with the swimbladder.

A number of other fishes have regressed, age-dependent swimbladders. These include such shallow-water marine fishes as certain gobies, blennies, flatfishes, and most muraenid eels (N. B.

Marshall, personal communication) and also some deep-sea fishes, such as certain species of *Cyclothone* and *Stomias,* whose swimbladders, upon regressing, become invested with fat (Marshall, 1960). As in stromateoids, the regression of the organ in these fishes is probably associated with habitat and/or internal changes. Swimbladder regression is eventually to be the subject of a general review.

Yet to be examined is the state of development of the swimbladder in newly-hatched stromateoid larvae. Since it is fully formed in fishes as small as 9 mm SL, the organ must develop quite early. The swimbladder may be of considerable importance to larvae in orientation and in positioning the body for food-capturing, although it is not known when the larvae begin to feed. Indeed, the swimbladder, as I judge from its particularly early regression in some stromateoids, may have its greatest functional significance in the larvae and smallest juveniles.

ACKNOWLEDGMENTS

I sincerely thank N. B. Marshall and Richard L. Haedrich for reading and offering suggestions on the manuscript. I am also grateful to Dr. Marshall for valuable advice on swimbladders and for providing space and facilities in the British Museum (Natural History). This work was supported by a NATO Postdoctoral Fellowship awarded by the National Science Foundation.

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BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. 30 NOVEMBER, 1970 NUMBER 360

MAMMALS FROM THE EARLY CENOZOIC OF CHUBUT, ARGENTINA

George Gaylord Simpson

ABSTRACT. *Angelocabrerus daptes*, new genus and species (Mammalia, Marsupialia, Borhyaenidae), *Coelostylodon florentinoameghinoi*, new genus and species (Mammalia, Notoungulata, ?Isotemnidae) and *Coelostylodon caroloameghinoi*, new species, are described from the Casamayor formation, probably early Eocene. Knowledge of upper premolars of *Didolodus* (Mammalia, Condylarthra, Didolodontidae) is increased and the status of *Acoelodus* (Mammalia, Notoungulata, Acoelodidae) is discussed. The latter genus and the family based on it are essentially indeterminate, and previous usage of the names is unjustified.

INTRODUCTION

A visit to Mar del Plata, Provincia de Buenos Aires, Argentina, early in 1970 enabled me for the second time to examine parts of the important collections of fossil mammals in the Museo Municipal de Ciencias Naturales of that municipality. In collections from the Casamayoran Stage of Chubut, three specimens were found to be of particular interest and to make especially important contributions to knowledge. The Director of the Museo, Sr. Galileo J. Scaglia, very kindly permitted me to study those specimens and to publish descriptions and discussions of them, presented herewith. I am again and increasingly indebted to Sr. Scaglia and to the whole staff of the Museo for their courtesy and cooperation. The accompanying illustrations were prepared by RaVae Marsh.

In the following, MMP precedes catalogue numbers of the Museo Municipal de Ciencias Naturales de Mar del Plata and MACN those of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires.

While carrying out the research for this paper I was employed jointly by the Museum of Comparative Zoology and the University of Arizona.

Order Marsupialia Illiger
Family Borhyaenidae Ameghino
Angelocabrerus, new genus

Etymology. For the late Angel Cabrera, a great mammalogist, who, among many other things, wrote an important study of borhyaenids. This kind of nomenclature is Ameghinian and is consonant with the related *Arminiheringia.* I have ventured to give the compound an appropriately masculine ending.

Type-species. Angelocabrerus daptes, new species, *infra.*

Known distribution. Casamayoran, Argentine Patagonia.

Diagnosis. Specialized borhyaenines. Canines with closed, rapidly tapering roots; short, heavy, fully enameled crowns. P_3 one-cusped, heavy, with small distinct talonid. M_{1-4} essentially two-cusped, with paraconid anterior and only slightly lingual to the larger protoconid. No trace of metaconid. Talonids unbasined, reduced to very slight, simple ledges. Protoconids and paraconids truncated with wear on M_{1-3}, becoming sharp points on M_4 with protoconid a high slender needle.

Discussion. As far as known, the dentition is similar to that of the much later (Santacrucian) *Borhyaena* and by the same token is also similar to the contemporary Casamayoran *Arminiheringia.* The talonid reduction seems to have gone even further in *Angelocabrerus* than in the other genera. The lower canine is unlike that of *Arminiheringia,* with a shorter closed root and more fully enameled crown. The way in which M_4 wears, quite distinctive from either *Arminiheringia* or *Borhyaena,* would seem to imply different occlusion and hence different structure in the unknown upper teeth, M^{3-4}, with which M_4 occluded. This wear is much as in *Plesiofelis,* considered by Cabrera (1927: 274-278) Deseadan in age and synonymous with *Pharsophorus* but almost certainly Mustersan and probably distinct from *Pharsophorus.* However, in *Plesiofelis* the molar talonids are considerably less reduced than in *Angelocabrerus.*

In *Arminiheringia auceta,* the only adequately known species of its genus, there is a rapid increase in size of the molars posteriorly, M_4 being about twice as large as M_1. The figures (somehow omitted in Simpson, 1948) are here given in Table 1. It is there shown that the increase is much less in *Angelocabrerus daptes,* with M_4 only about half again as large as M_1. The increase

is even less in *Borhyaena*. As far as the evidence goes, *Angelocabrerus* could be ancestral to *Borhyaena*, and in that case the rate of evolution in known parts must have been extremely slow. Knowledge of the present genus is too incomplete, however, to warrant a firm conclusion.

As in *Arminiheringia* and *Borhyaena* but to even more marked degree, P_3 is a large and heavy tooth. It here approximates M_3 in dimensions. It has a single main cusp, with a long anterior and short, nearly vertical posterior slope. There is a minute cuspule at the anterior base. There is a distinct but small, shelflike talonid with a single cuspule. This is absent in *Borhyaena* and also in the only known specimen of *Arminiheringia* that might show it, but the latter is so worn that a small talonid could have been present originally. Except for the points already mentioned, the lower molars are like *Arminiheringia* and *Borhyaena* in structure.

Angelocabrerus daptes, new species.

Etymology. Greek *daptes*, eater, gnawer, from the inferred carnivorous, possibly ossifragous habits of the animals.

Holotype. MMP 967M, part of right mandibular ramus with M_{2-4}, left P_3, M_1, and M_2 probably of the same individual, two lower canines somewhat broken, and small caniniform tooth and tip of another doubtfully associated.

Hypodigm. Holotype only.

Horizon and locality. Casamayoran, south of Lago Colhué-Huapí, Chubut, Argentina. The specimen was a surface find high in the beds, and derivation from an overlying formation is possible but quite improbable.

Diagnosis. Only known species of the genus as diagnosed above.

Discussion. The loose left M_2 has somewhat darker enamel and is slightly less worn than the right M_2 in the mandibular fragment. Its color and wear are more consonant with those of the loose teeth identified as left P_3 and M_1. However, there can be little serious doubt that those and the two loose lower canines do in fact belong to the same individual as the mandibular fragment. All were found together, they are congruent in size and structure, and they add up to a unique specimen of a group extremely rare in these beds. The two slender caniniform teeth are dubious and I do question whether they belong to the same animal.

The diagnosis and discussion of the genus and the illustrations make further description unnecessary.

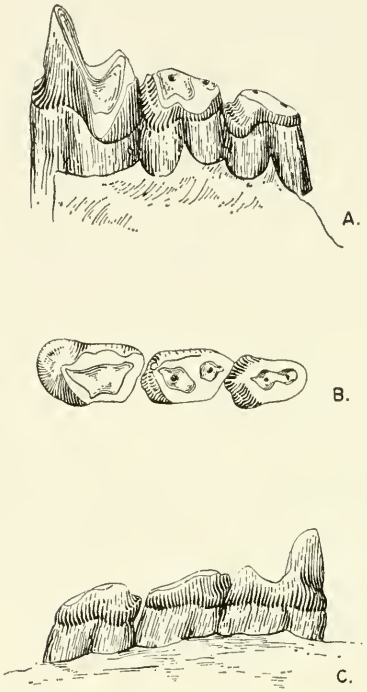

Figure 1. *Angelocabrerus daptes,* new genus and species. Holotype, MMP 967M. Right $M_{2\text{-}4}$. A, buccal view. B, occlusal view. C, lingual view. × 1.

Order Condylarthra Cope
Family Didolodontidae Scott
Didolodus sp. indet.

Specimen. MMP 696M, fragment of right maxilla with $P^{2\text{-}4}$.

Horizon and locality. Casamayoran of Cañadón Vaca, tributary to the left (northwest) bank of the Río Chico, Chubut, Argentina.

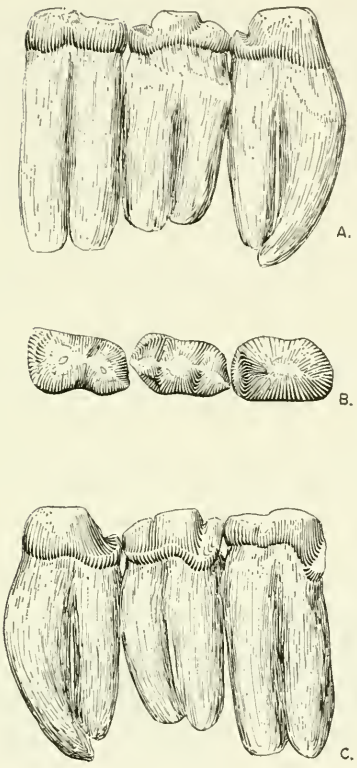

Figure 2. *Angelocabrerus daptes,* new genus and species. Holotype, MMP 967M. Left P_3 - M_2. A, lingual view. B, occlusal view. C, buccal view. × 1.

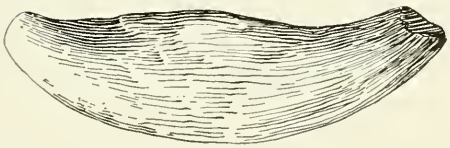

Figure 3. *Angelocabrerus daptes,* new genus and species. Holotype, MMP 967M. Lower canine. × 1.

Discussion. This specimen is interesting because it shows the coronal structure of P^{2-4} of *Didolodus* in relatively little worn condition and because the proportions of these teeth are distinctive.

Comparison is mainly with MACN 10690, holotype of *Didolodus multicuspis* Ameghino, the only other specimen of *Didolodus* known to me that includes P^{2-4}. It is figured in Simpson, 1948, text figures 25 and 26 and plate 10, figures 1 and 2. MACN 10738 includes P^2, which has not been figured but was included in my description of *D. multicuspis* (Simpson, 1948: 101). AMNH 2847 is a P^3 referred to *D. minor* by me (Simpson, 1948: 103) but not separately described or figured.

As shown in Table 2, P^2 and P^4 are each shorter than in the holotype by 7 per cent, which does not in itself suggest specific distinction, and P^3 has almost the same length in the two specimens. However, all three teeth are more notably narrower in MMP 696M, by 16 per cent, 20 per cent, and 19 per cent for P^2, P^3, and P^4 respectively. A result is that all three teeth are longer relative to their widths in MMP 696M. This is especially notice-

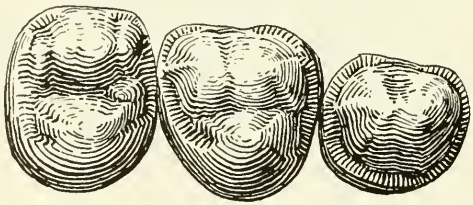

Figure 4. *Didolodus* sp. MMP 696M. Right P^{2-4}, occlusal view. × 3.

able in P^3, which is distinctly transverse in MACN 10690 but equidimensional in MMP 696M. P^3 of AMNH 28471, referred to *D. minor,* is even more transverse than in the holotype of *D. multicuspis.* Its width slightly exceeds that of P^3 in MMP 696M, although its length is decidedly (25 per cent) shorter. The individual represented by MMP 696M was probably closer to *D. multicuspis* in over-all size, but the differences in some dimensions and in proportions make reference doubtful either to that species or to *D. minor.* At the same time, they do not warrant definition of a new species, which in any case should preferably not be based on upper premolars, for which there is so little comparative material.

Specimens of known origin referable to *D. multicuspis* without much doubt are all from south of Lago Colhué-Huapí, and those similarly referable to *D. minor* are from Cañadón Vaca. MMP 696M is from Cañadón Vaca but probably does not belong to *D. minor*. Specimens and field data for *Didolodus* are still far from sufficient for identification of populations within the genus and for determination of their distribution.

P^2 of MMP 696M, unlike the less well-preserved specimens previously known, is seen to have two distinct external cusps, connate above the tips but still separated by grooves. These are at least descriptively paracone and metacone, and the metacone is only slightly lower and smaller than the paracone. The tooth is completely surrounded by a cingulum, but this is feeble on the middle of the labial face. The lingual slope from paracone plus metacone to the labial cingulum is slightly uneven, but is without really distinct cusps. P^3 and P^4 also have distinct paracone and metacone but, unusually, the metacone is lower and smaller relative to the paracone progressively from P^2 to P^4. P^3 and P^4 have well-developed protocones, and the cingula do not cross their lingual faces. A distinct cingular cusp or style is present on each tooth anterior and slightly labial to the paracone and there is a similar but smaller and less distinct cuspule posterior to the metacone. Each tooth has a distinct protoconule but no metaconule. There is no hypocone. It is also unusual that P^4 is distinctly shorter than P^3, although wider.

The structure of P^2 in this specimen seems to be rather different from that in the holotype of *D. multicuspis* and more molariform. Except for dimensions and proportions, apparent differences in structure of P^{3-4} are possibly due only to the more worn condition of the holotype of *D. multicuspis*.

Although far from identical, there is considerable resemblance between P^{2-4} of MMP 696M and the homologous teeth of North American *Phenacodus*. A fairly close ancestral relationship is confirmed to that extent. However, considerable independent evolution is also suggested. For example, P^{2-3}, especially, of MMP 696M, are more distinctly molariform than their homologues in *Phenacodus*.

Order Notoungulata Roth
Family Isotemnidae Ameghino
Coelostylodon, new genus

Etymology. Greek *koilos,* hollow, *stylos,* pillar, *odon,* tooth. The name is meant to recall former reference to *Acoelodus* and resemblance to *Pleurostylodon.* It is also consonant with much Ameghinian nomenclature.

Type-species. Coelostylodon florentinoameghinoi, new species, *infra.*

Known distribution. Casamayoran, Argentine Patagonia.

Diagnosis. Primitive notoungulates with complete, nearly closed dentition. Upper canine small and fully incisiform. Cheek teeth brachydont, P^2-M^3 soon wearing so that crown presents a single fossa, without complex folds or anterior opening. M^{1-3} with flattened, slightly bifid lingual faces. M^{1-3} with slight parastyle and paracone folds and very feeble metacone swelling on ectolophs, no mesostyle. M^3 subtriangular, with short but distinct metaloph, longer than M^1 or M^2 and almost as long as broad.

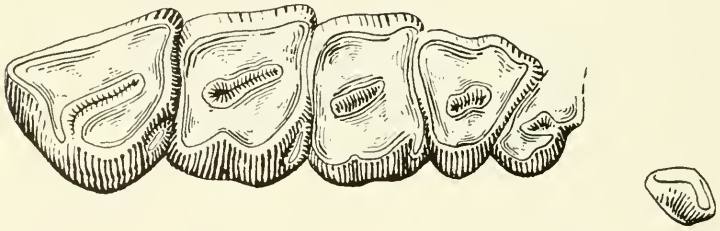

Figure 5. *Coelostylodon florentinoameghinoi,* new genus and species. Holotype, MMP 1723M. Right C and P^3 - M^3. × 1½.

Discussion. This genus is essentially that called *Acoelodus* by Ameghino (1901: 467) and discussed by me (Simpson, 1967: 57) under that name, but that application of the name can no longer be sustained. The type-species of *Acoelodus* is *A. oppositus* Ameghino, 1897 (p. 454). The holotype of that species is MACN 10770, a fragment of a left mandibular ramus with much worn P_{2-3} and part of P_4. That specimen is essentially indeterminate. In 1901 Ameghino referred to the species a poorly preserved skull, MACN 10753, and redefined the genus essentially on the basis of

that specimen. Desiring to validate as much as possible of Ameghino's nomenclature, I accepted the reference and redefinition, taking MACN 10753 as essentially a neotype in Ameghino's usage and designating it as such (Simpson, 1967: 58). However, that action is invalid under the present code of nomenclature (Stoll *et al.,* 1964, Article 75) because in fact the holotype, MACN 10770, has not been lost or destroyed.

If now there were a reasonable probability that the referred skull and the holotype belong to the same genus and species, the type designation would have no practical importance and one could continue to use the name *Acoelodus* for the genus and *A. oppositus* for the species represented by the referred skull. In fact, however, as I already mentioned in previous discussion (1967), there is no good evidence that the two specimens are of the same genus and species, and there is some contrary evidence. The contrary evidence is weightier than I previously indicated. If the comparative sizes of $P_{2\text{-}3}$ and $P^{2\text{-}3}$ in *Acoelodus* were approximately as in *Pleurostylodon,* a reasonable assumption, then $P^{2\text{-}3}$ of the skull MACN 10753 are some 22 to 44 per cent larger in various dimensions than would be expected from the holotype of *Acoelodus oppositus* and are also different in relative sizes and proportions. It is thus highly improbable that the two specimens are conspecific, and if they are not conspecific, there is no reason to consider them congeneric.

The genus represented by the holotype of *Acoelodus oppositus* is indeterminate, a notoungulate *incertae sedis* as far as my knowledge and judgment go. The genus represented by MACN 10753 is determinate and is distinct from any other for which there is comparable material known to me. This conclusion is reinforced by discovery of another specimen, MMP 723M, that can be referred to the same genus as MACN 10753 but is specifically distinct. In order to avoid possible further confusion with *Acoelodus,* the species represented by MMP 723M is made type-species for the new generic name.

In order to avoid still another confusion, it must be noted that none of Ameghino's figures labeled *"Acoelodus oppositus"* in several of his publications are conspecific or congeneric either with the holotype of that species or with MACN 10753 (for details and discussion see Simpson, 1967: 58-59).

Ameghino considered *Acoelodus* as closely related to *Oldfieldthomasia* and so placed the latter in his family Acoelodidae, but

that was based on specimens dubiously or incorrectly referred to *Acoelodus,* including at least one that in fact belongs in *Oldfieldthomasia.* Since the holotype of the type-species of *Acoelodus* is not identifiable as to family, the name Acoelodidae has no established significance. For that reason, I named a family Oldfieldthomasiidae for *Oldfieldthomasia* and its probable relatives (Simpson, 1945: 126). In revision of the Casamayoran fauna, I put MACN 10753, under the incorrect reference name *Acoelodus oppositus,* in the Oldfieldthomasiidae. The genus *Coelostylodon,* to which that specimen is now referred as holotype of *C. caroloameghinoi,* is of uncertain family position. It differs from all adequately characterized previously named genera of both the Oldfieldthomasiidae and the Isotemnidae, but has resemblances to both families. Present reference to the Isotemnidae is very tentative. The upper molar structure is most nearly similar to that of *Pleurostylodon,* an isotemnid, among adequately known genera, but *Coelostylodon* differs from *Pleurostylodon* and other isotemnids in its small, incisiform canine and various other details. The canine is more like that of *Oldfieldthomasia,* but the molars are quite different.

Coelostylodon florentinoameghinoi, new species

Etymology. For Florentino Ameghino, famed describer of most of the Casamayoran fauna. Combination of given and family names is a nomenclatural device that he often used.

Holotype. MMP 723M, nearly complete but badly crushed skull.

Hypodigm. The holotype only.

Horizon and locality. Lowest Casamayoran beds in the barranca south of Lago Colhué-Huapí, Chubut.

Diagnosis. Significantly larger than *C. caroloameghinoi* (see Table 3). Posterolabial angle of M^3 less projecting.

Discussion. The teeth are deeply worn in both of the holotypes now referred to this genus. As preserved, there is no marked, discernible difference in structure of the cheek teeth. MMP 723M clearly has the small canine considered characteristic of the genus. P^{1-2} are almost completely fragmented, but seem to have been quite small, perhaps more so, relatively, than in MACN 10753. The posterolabial corner of M^3 does not project so distinctly as in MACN 10753.

The skull is too badly crushed to make out much significant detail. It seems to have been a primitive, unspecialized notoungulate skull generally similar to that of *Pleurostylodon*.

Coelostylodon caroloameghinoi, new species.

Acoelodus oppositus, in error, Ameghino, 1901: 365; Simpson, 1967: 58 and plate 11, fig. 1.

Etymology. For Carlos Ameghino, who discovered the Casamayoran fauna and found the holotype of this species.

Holotype. MACN 10753, poorly preserved anterior part of skull.

Hypodigm. The holotype only.

Horizon and locality. Casamayoran, barranca south of Lago Colhué-Huapí.

Diagnosis. Significantly smaller than *C. florentinoameghinoi* (see Table 3). Posterolabial angle of M^3 sharply produced posteriorly (or distally).

Discussion. In 1901 and thereafter Ameghino based his concept of *Acoelodus oppositus* mainly on this specimen, but he did not figure it, and none of the specimens figured by him as *Acoelodus oppositus* belong to the present genus or species. The holotype is adequately figured in my previous memoir, as cited above.

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TABLE 1

Measurements in millimeters of teeth of *Angelocabrerus* and allied borhyaenids.

		Angelocabrerus daptes Holotype, MMP 967M		*Arminiheringia auceta* Holotype MACN 10970*	*Arminiheringia contigua* Holotype MACN 10319	*Borhyaena tuberata* Princeton 15701†
		Right	Left			
P_3	Length	—	12.4	11½	10.7	14.3
	Width	—	7.4	7½	—	6.5
M_1	Length	—	9.8	9½	7.8	12
	Width	—	6.3	7	—	6
M_2	Length	10.5	10.4	12	—	12
	Width	7.2	7.1	7½	—	7
M_3	Length	12.8	—	15	—	13
	Width	7.9	—	10	—	7½
M_4	Length	14.4	—	21	—	16
	Width	10.4	—	12½	—	9

*Measurements taken by me to the nearest half millimeter, the condition of the specimen suggesting that the apparent accuracy of measurements to a tenth of a millimeter would be spurious.

†Measurements from Sinclair (1906). It appears that Sinclair measured P_3 to tenths but M_{1-4} to half millimeters.

TABLE 2

Measurements in millimeters of upper premolars of *Didolodus*.

		D. multicuspis MACN 10690	*D. minor* AMNH 28471	*D.* sp. MMP 696M
P^2	Length	7.6	—	7.1
	Width	7.4	—	6.2
	L/W	1.03	—	1.15
P^3	Length	7.5	5.7	7.6
	Width	9.5	7.8	7.6
	L/W	.79	.58	1.00
P^4	Length	7.0	—	6.5
	Width	10.0	—	8.1
	L/W	.70	—	.80

TABLE 3

Comparative measurements in millimeters of dentitions of holotypes of *Coelostylodon florentinoameghinoi* and *C. caroloameghinoi*.

		C. florentinoameghinoi MMP 723M	*C. caroloameghinoi* MACN 10753
P^4	Length	9.9	7.5
	Width	12.5	9.9
M^1	Length	Ca.10	8.0
	Width	15.4	11.5
M^2	Length	12.6	8.5
	Width	17.0	11.8
M^3	Length	15.1	10.0
	Width	15.4	10.7

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. 30 NOVEMBER, 1970 NUMBER 361

ADDITIONS TO KNOWLEDGE OF THE ARGYROLAGIDAE (MAMMALIA, MARSUPIALIA) FROM THE LATE CENOZOIC OF ARGENTINA

GEORGE GAYLORD SIMPSON

ABSTRACT. A recent monograph of the Argyrolagidae is supplemented by observations on specimens not previously seen by the author. The holotype of *Argyrolagus palmeri* confirms previously published data. An additional specimen of *Argyrolagus scagliai* adds to knowledge of the coronal pattern of lower molars. *Argyrolagus parodii* is a hitherto dubious species the holotype of which was destroyed. A second specimen is made neotype; it validates the species and permits redefinition.

A monograph of the Argyrolagidae (Simpson, 1970) was completed early in 1968 and an addendum included late in that year. Early in 1970 a visit to Argentina made possible the study of several specimens not available or not known to me when the monograph and addendum were written. These add significantly to knowledge of the family.

For the facilities for making and the privilege of publishing these observations I am greatly indebted to the authorities of the Museo de La Plata and especially to Dr. Rosendo Pascual and Sr. Jorge Zetti. The accompanying photographs were made under the direction of Sr. Zetti and provided for this publication by the Museo. In Buenos Aires Sr. Guillermo del Corro courteously made available the type of *Argyrolagus palmeri*. The drawing was made by RaVae Marsh from a sketch by me. While making this study I was employed jointly by Harvard University and the University of Arizona.

In the following all measurements are in millimeters: L = length (anteroposterior or mesiodistal). W = width (bucco-lingual). L_a = length of trigonid. L_p = length of talonid. W_a = width of trigonid. W_p = width of talonid. MACN = Museo Argentino de

Ciencias Naturales "Bernardino Rivadavia." MLP = Facultad de Ciencias Naturales y Museo de La Plata. MMP = Museo Municipal de Ciencias Naturales de Mar del Plata.

Family Argyrolagidae Ameghino, 1904
Genus *Argyrolagus* Ameghino, 1904
Argyrolagus palmeri Ameghino, 1904

Holotype. MACN A53-4, part of left mandibular ramus, originally with I_1 and M_{1-4}, collected by Carlos Ameghino at Monte Hermoso in 1904.

Remarks. For other formal data see Simpson, 1970: 11. When that account was written I had not seen the type, which is in the Ameghino Collection in Buenos Aires and catalogued as above. I_1 has been lost since the specimen was figured by F. Ameghino (1906, fig. 221) and L. Kraglievich (1931, fig. 2). Both of those figures represent the specimen accurately. New measurements on the specimen agree reasonably well with those taken from the earlier figures (given in Simpson, 1970, Table 1), see present Table 1.

Argyrolagus scagliai Simpson, 1970

Addition to hypodigm. MPL 49-IX-7-1, right mandibular ramus with alveoli of I_{1-2} and P_3 and all of M_{1-4}. "Miramar, prov. de Bs. Aires," probably Chapadmalal formation. Presented to the MLP by the widow of Dr. Santiago Roth in August, 1924.

Description. For formal data on the species see Simpson, 1970: 12. This specimen has M_{1-4} beautifully preserved and less worn than in others known. In this genus the hypselodont molars rapidly lose the coronal pattern by wear and become columns with characteristic outline but no internal structure. Here even M_1, although somewhat worn, preserves some coronal features. M_4 is also fully erupted and beginning to wear. The teeth do not taper in the alveoli and would not increase in size with wear. The dimensions of the exposed ends of these young teeth are comparable with those of old individuals of the species (see Table 2). All the molars retain traces of a fossettid in the trigonid. M_1 has a somewhat more complex outline than in other, individually older specimens considered to be of the same species (see Fig. 2). Most of the crown is horizontally truncated by wear, but there is a steeply sloping anterolingual wear facet. On the anterior face

there is a well-developed cingulum, not yet worn, enclosing a small pocket. The preservation makes possible separate trigonid and talonid measurements in Table 3.

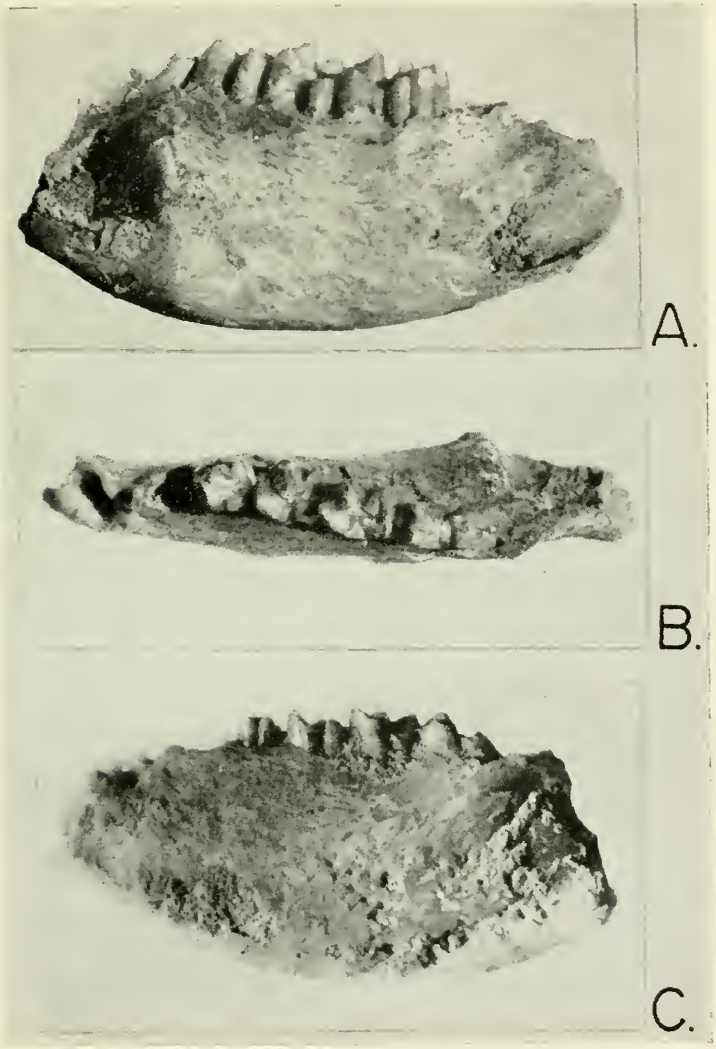

Figure 1. *Argyrolagus scagliai* Simpson, 1970. M.L.P. No. 49-IX-7-1, right mandibular ramus with M_{1-4}. A, buccal view. B, occlusal view. C, lingual view. Approximately × 4¼.

Figure 2. *Argyrolagus scagliai* Simpson, 1970. M.L.P. No.49-IX-21, right M_1. Occlusal view, diagrammatic sketch. Approximately × 10.

Argyrolagus parodii Rusconi, 1933

Neotype. MLP 62-VII-27-81, right mandibular ramus with I_1, alveolus of I_2, and P_3-M_4, from the Playa las Palomas, near the Balneario Chapadmalal. Collected by the personnel of MLP in August, 1961.

Revised diagnosis. Smaller than *A. palmeri* or *A. scagliai.* Trigonids somewhat more triangular, paraconids medial. Talonids relatively short. Labial and lingual sulci directly opposite. Talonid of M_1 somewhat reduced, but decidedly larger than in *Microtragulus.* Buccal extension of coronoid crest strong.

Discussion. In a letter written shortly before his lamented death, Sr. Rusconi informed me that the holotype of this species, in his private collection, had been destroyed. The available figures and description of that holotype are somewhat equivocal, as discussed in Simpson, 1970: 14-15. There is little doubt, however, that MLP 62-VII-27-81 does belong to the same species. It is very close to the size indicated by Rusconi in text and figures, as here shown in Table 4, and it also shares the most likely morphological distinctions of the holotype. The present specimen can be confidently referred to *Argyrolagus* and it shows that *A. parodii* is distinct from any other known species—both points left in some doubt by the destruction of the holotype. This case meets all the conditions for designation of a neotype set forth in Article 75(a) of the International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology, and the present treatment supplies all the qualifying conditions specified in Article 75(c) of the Code.

The locality where the holotype was found is not precisely known but was somewhere along the shore four or five kilometers

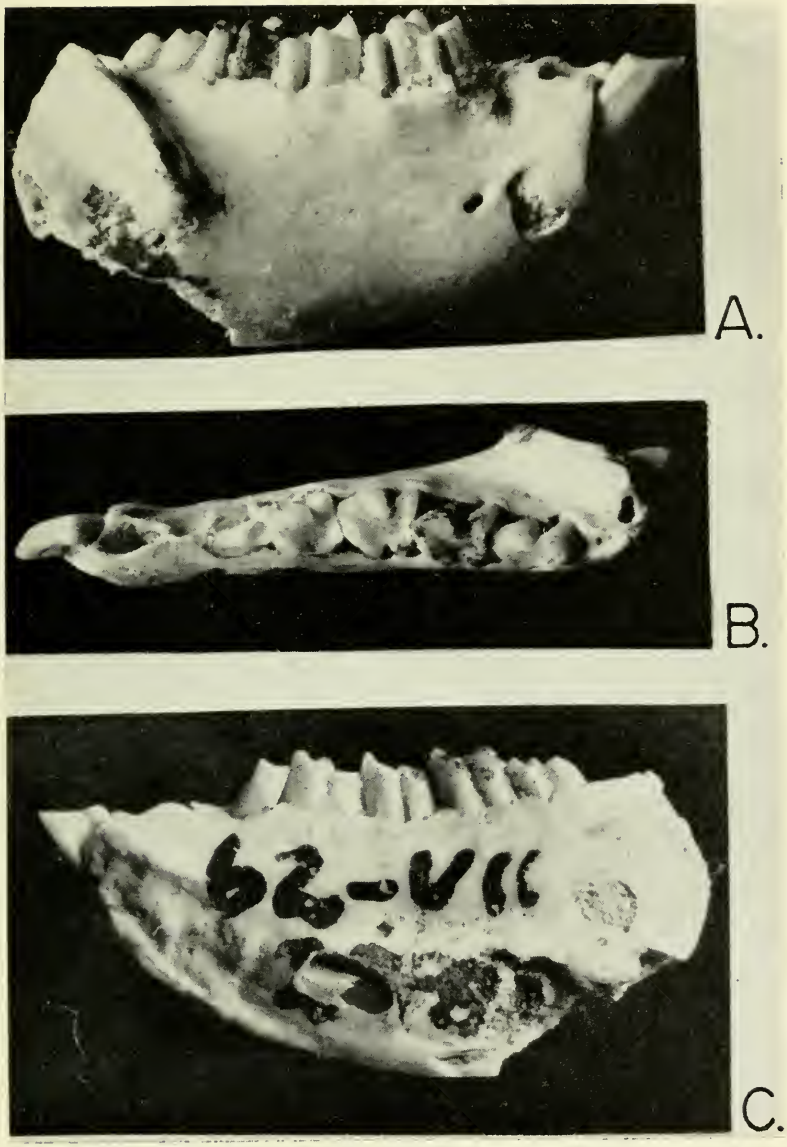

Figure 3. *Argyrolagus parodii* Rusconi, 1933. Neotype, M.L.P. No. 62-VII-27-81, right mandibular ramus with I_1 and P_3 - M_1. A, buccal view. B, occlusal view. C, lingual view. Approximately × 6.

northeast of Miramar, Buenos Aires Province. The neotype is from the same sequence of exposures on the shore about 12½ to 13½ kilometers farther northeast. The holotype was probably from the Chapadmalal formation, as restricted, but possibly Vorohué. (See J. L. Kraglievich, 1952.) There is no clearly

Figure 4. Argyrolagidae, genus and species undetermined. M.L.P. No. 59-IX-28-98, right tibiofibula lacking unfused portion of fibula. A, lateral view. B, anterior view. C, medial view. D, posterior view. Approximately × 2.

established difference between the faunas of the two formations. The neotype is almost certainly from the restricted Chapadmalal formation. The two are probably of the same age, and in any case can hardly have a faunally appreciable difference in age.

The specimen now made neotype of *Argyrolagus parodii* is the one figured, without catalog reference, as *Microtragulus argentinus* by Ringuelet (1966, plate X, figs. I, J) and used as a basis (*Ibid.*, pp. 58-59) for redefinition of the genus *Microtragulus* (taken as a synonym of *Argyrolagus*) and the family Microtragulidae (equated with Argyrolagidae). As previously pointed out (Simpson, 1970: 65-67), the redefinitions are valid for the specimen in question but are too restricted for the genus and family as wholes.

The preceding diagnosis and accompanying measurements (Table 4) and photographs (Fig. 3) make detailed description unnecessary.

Argyrolagidae gen. et sp. indet.

MLP 59-IX-28-98 is a tibiofibula lacking the free part of the fibula, collected by Dr. J. Frenguelli from the "Chapadmalense" of Baliza Chica, northeast of Miramar. At this locality it would be either from a very high level in the Chapadmalal formation, restricted, or from the overlying Vorohué formation. Its length is 53.5 mm, compared with 60.4 mm for MMP 7855, holotype of *Argyrolagus scagliai*. It also differs from the latter in that the proximal part of the cnemial crest ends abruptly slightly below rather than at the articular surfaces and also ends abruptly distally rather than passing gradually into the shaft. This specimen may belong to *Microtragulus reigi*, but association cannot now be established.

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TABLE 1

Measurements of teeth of holotype of *Argyrolagus palmeri*

	M_1		M_2		M_3		M_4		LM_{1-4}
	L	W	L	W	L	W	L	W	
MACN A53-4	1.9	1.1	2.1	1.3	2.0	1.3	2.0	1.1	7.8

TABLE 2

Comparative measurements of teeth of *Argyrolagus scagliai*

	M_1		M_2		M_3		M_4		LM_{1-4}
	L	W	L	W	L	W	L	W	
Holotype, MMP 7855	1.7	1.4	2.0	1.7	2.0	1.6	2.2	1.2	8.5
MLP 49. IX. 7.1	1.8	1.7	2.3	1.9	2.3	1.8	2.2	1.4	8.6

TABLE 3

Trigonid and talonid measurements of *Argyrolagus scagliai*, MLP 49.IX.7.1.

M_1				M_2				M_3				M_4			
L_a	L_p	W_a	W_p	L_a	L_p	W_a	W_p	L_a	L_p	W_a	W_p	L_a	L_p	W_a	W_p
1.2	0.6	1.6	1.7	1.4	0.9	1.9	1.9	1.5	0.8	1.8	1.6	1.3	0.9	1.4	1.3

TABLE 4

Measurements of destroyed holotype of *Argyrolagus parodii*, from text and figures of Rusconi, and of neotype MLP 62-VII.27.81.

	M_1		M_2		M_3		M_4		LM_{1-4}
Holotype:	L	W	L	W	L	W	L	W	
Rusconi, 1933, text	—	—	—	—	1.9	—	1.3	—	—
Rusconi, 1933, fig. 1a	—	—	—	—	1.8	1.6	1.6	1.2	—
Rusconi, 1936, fig. 12	—	—	—	—	1.6	1.4	1.6	1.2	—
Neotype	1.6	1.4	1.8	1.5	1.7	1.4	1.7	1.1	6.7

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Museum of Comparative Zoology

CAMBRIDGE, MASS. 30 NOVEMBER, 1970 NUMBER 362

ADDITION TO KNOWLEDGE OF *GROEBERIA* (MAMMALIA, MARSUPIALIA) FROM THE MID-CENOZOIC OF ARGENTINA

George Gaylord Simpson

ABSTRACT. *Groeberia pattersoni*, new species, from the Divisadero Largo formation, is based on the second known specimen of that genus. Some information on the hitherto unknown skull of genus and family is provided. Reference to the Marsupialia is supported, but affinities within the Marsupialia remain dubious.

The extraordinary fossil marsupial genus *Groeberia* has hitherto been known from a single specimen, a fragmentary mandible, named and described by Patterson (1952). A second specimen was found by Dr. Edgardo Rolleri of the Yacimientos Petrolíferos Fiscales (Argentine government petroleum bureau) and deposited in 1968 in the Museo de La Plata. Dr. Rosendo Pascual kindly referred it to me for study, which I carried out in La Plata early in 1970, and for publication, here presented. Sr. Jorge Zetti, assistant to Dr. Pascual, facilitated the study and arranged for photographs, provided by the Museo for this publication. The accompanying drawings were made by RaVae Marsh on the basis of sketches by me. I am also indebted to Dr. A. J. Amos, Dean of the Faculty of Natural Sciences and the Museum of La Plata, and to Sr. G. J. Scaglia, Director of the Museo Municipal de Ciencias Naturales of Mar del Plata, who sent the holotype of *G. minoprioi* on loan to La Plata for direct comparison with the present specimen.

The research for this paper was performed while I was employed jointly by the University of Arizona and the Museum of Comparative Zoology.

Class Mammalia Linnaeus, 1758
Order Marsupialia Illiger, 1811
Family Groeberiidae Patterson, 1952
Genus *Groeberia* Patterson, 1952
Groeberia pattersoni, new species

Etymology. For Bryan Patterson, who named and described the genus and its type-species, *G. minoprioi*.

Holotype. Museo de La Plata No. 68-VI-27-1, partial skull and mandible.

Hypodigm. Holotype only.

Horizon and locality. Divisadero Largo formation, [in the general vicinity of] Mina Atalá, Mendoza, Argentina.

Diagnosis. Anterosuperior part of symphysis much more slender and incisors smaller than in *G. minoprioi*. M_{3-4} also, but less, smaller. See Table 1.

Identification. The holotype of the type-species *Groeberia minoprioi* includes most of the mandibular symphysis and incisors, left M_{2-3}, and broken bases of M_1 and M_1 (see Patterson, 1952). The present specimen also preserves most of the symphysis and lower incisors and has the broken bases of left M_{3-4}. These parts are morphologically closely similar in the two specimens and quite unlike any other animal known to me. Reference to the same genus is indicated. Both are from the Divisadero Largo formation and

TABLE 1

Comparative measurements in millimeters of holotypes of *Groeberia minoprioi* and *G. pattersoni*.

	G. minoprioi	*G. pattersoni*
Transverse at narrowest part of symphysis, at postincisive diastema	ca. 5.8	ca. 3.4
Transverse, across both incisors at alveoli	ca. 5.8	ca. 3.4
M_3 Length	2.3	ca. 1.8
M_3 Width	1.6	ca. 1.4
M_4 Length	ca. 2.3	ca. 1.5
M_4 Width	ca. 1.8	ca. 1.3

Measurements of M_3 of *G. pattersoni* and of M_4 of both specimens are on broken bases of teeth and are rough approximations.

near the same locality: the holotype of *G. minoprioi* from one-half kilometer east of the Cerro Divisadero Largo (Patterson, 1952: 3) and that of *G. pattersoni* recorded as "Mina Atalá," which would be about 1¼ kilometers northeast of the previous locality but which must be a rough approximation, as the Mina Atalá is not on the Divisadero Largo formation.

The holotype of *G. minoprioi* is from Minoprio's stratum F (see map and stratigraphic discussion in Simpson, Minoprio, and Patterson, 1962). The level of the present specimen is not so precisely known. Although no faunal change has been demonstrated within the formation, its deposition may have covered a considerable span of time and the two specimens may not be very closely contemporaneous. There is some presumption that specimens so similar in morphology and provenience are conspecific, but, as far as I know, the difference in slenderness of the symphysis and sizes of the teeth are greater than within adults of any one species of marsupials. This difference can hardly be due to greater age of the holotype of *G. minoprioi*. The incisors of the holotype of *G. pattersoni* do not taper in the alveoli, hence they could age considerably without increasing in diameter at the alveoli. Although measurements are imprecise, the length of M_1 is about 50 per cent longer in the holotype of *G. minoprioi*, and these brachydont teeth do not grow after eruption. The holotype of *G. pattersoni* evidently had all teeth erupted and some skull sutures closed, as in fully adult animals. Thus specific separation is indicated.

Age. Simpson, Minoprio, and Patterson (1962: 290) concluded that "the age of the Divisadero Largo fauna is approximately early Deseadan or latest pre-Deseadan," but that knowledge at that time did not warrant basing on it the apparently missing mammalian age-stage between Mustersan and Deseadan. However, on evidence not fully stated, Pascual, Ortega, Gondar, and Tonni (1965) proposed a "Divisaderense" (in English, Divisaderan) mammal age-stage as intermediate between Mustersan and Deseadan and separated from each by a hiatus. They tentatively correlated it with the Ludian of Europe and Duchesnian of North America as latest Eocene. As those authors also did recognize, the data do not really permit close correlation, and I believe that all one can now say is that the age in terms of the European epochs may be somewhere around late Eocene or early Oligocene, hence, in terms of absolute age, more or less middle Cenozoic.

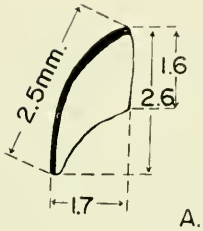
Description. As found, the specimen included at least the anterior part of the skull and most of the mandible in articulation. Some time before the specimen came into the control of the Museo de La Plata, the skull and mandible were separated and both were severely damaged. Nevertheless, what remains adds considerably to knowledge of this remarkable and enigmatic genus.

The two lower incisors are preserved for a length of about 12 mm within their alveoli. The anterior ends are broken and the posterior ends have been ground smooth, presenting the appearance seen in Figure 1B. The pulp cavity is here open, and there is no sign of root formation, so these teeth were clearly hypselodont,[1] as in *G. minoprioi*. The teeth curve so that the posterior parts were nearly horizontal, in an odd medial posterior projection of the symphsis, and the extra-alveolar parts would have been nearly vertical. Enamel is lacking on the medial and dorsal faces, and at this depth in the alveoli even the dentine has not quite closed the pulp cavity dorsally. Heavy enamel occurs ventrally, and this extends, thinning as it goes, onto the lateral faces, more so than in the extra-alveolar parts of the incisors of the holotype of *G. minoprioi*.

There is a short diastema posterior to the lower incisors and then a series of cheek teeth, probably four as in *G. minoprioi*, although here they cannot be definitely counted. The bases of what are almost certainly the last two cheek teeth can be made out, but the crowns are not visible. These teeth are brachydont as in *G. minoprioi* and similar in outline but perhaps slightly less elongate.

There are two pairs of upper incisors, here designated I^1 and I^2 for convenience, although their ancestral homologies are unknown.

[1] Dictionaries give "hypselodont" as a variant of "hypsodont," and the most recent authoritative odontology, Peyer (1968), uses "hypselodont" in place of "hypsodont." It is, however, more convenient to adopt a distinction sometimes made by mammalogists, especially paleomammalogists. I define as *hypsodont* a tooth that eventually develops one or more roots but that has a crown definitely higher than those roots or than any of its horizontal dimensions and, as *hypselodont*, a tooth that never forms a root but continues to grow and to extrude new parts from the alveolus throughout life. Peyer was not a mammalogist and devoted relatively little attention to mammal teeth. Other odontologists have often oriented their work on groups, especially *Homo*, in which hypselodont teeth (in my sense) do not occur. The distinction is of great functional importance.



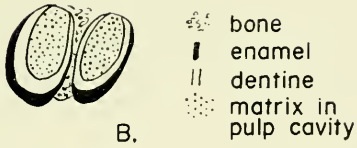


Figure 1. *Groeberia pattersoni*, new species. Holotype, M.L.P. No. 68-VI-27-1. A, sketch and measurements of wear surface of I^1, approximately × 6. B, sketch of posterior (intra-alveolar) exposure of paired lower incisors, approximately × 5.

I^1 is a large, strongly curved tooth with an alveolus extending posterodorsally far back in the facial region to above the infraorbital foramen. It and I^2 are probably both hypselodont. The cross section is peculiar, with an oblique, long, slightly convex, buccal, enamel-covered face; a flat, anteroposterior, enamelless, anteromedial face; and a likewise enamelless, concave, posteromedial face. The three faces meet at definite angles, approximately right angles at both ends of the anteromedial face but strongly acute between the buccal and posteromedial faces. (See Fig. 1A.) The enamel is nearly smooth but with slight wavy longitudinal ribbing. Right and left I^1 are close to each other on their medial faces.

I^2 is much smaller than I^1, measuring about 1.1 mm across the buccal face as compared with about 2.5 mm for I^1. I^2 is also enameled on the buccal face, and probably not elsewhere. The cross section cannot be clearly determined as the specimen is preserved. I^2 is less curved longitudinally than I^1 and although

the extra-alveolar parts of the two are in contact, the alveoli diverge. In the most probable orientation of the skull, the extruded part of I^1 is slightly recumbent and that of I^2 is nearly vertical.

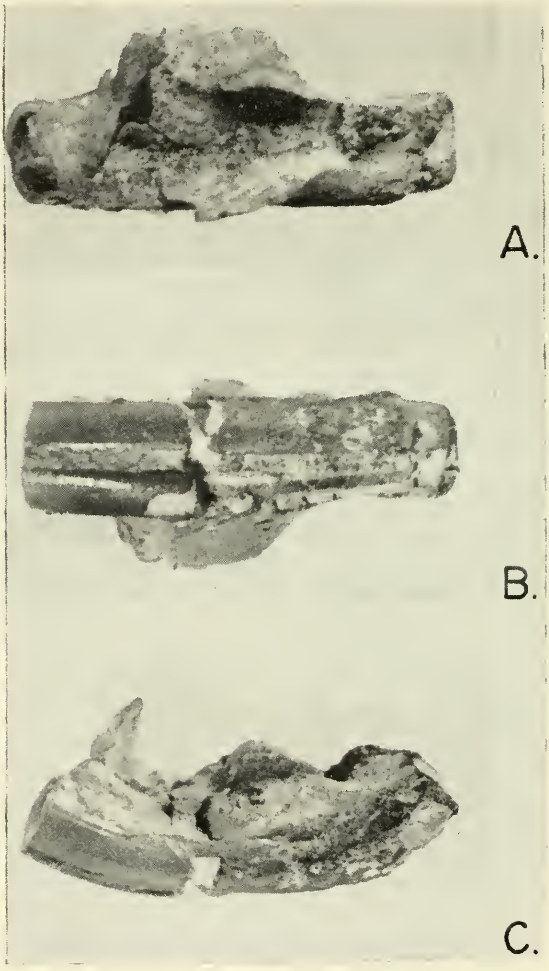


Figure 2. *Groeberia pattersoni*, new species. Holotype, M.L.P. No. 68-VI-27-1. Fragment of symphysis with parts of lower incisors. A, supero-posterior or lingual view. B. infero-anterior or genial view. C, right lateral view (in more anatomical orientation the anterior parts of the incisors would be nearly vertical). Approximately × 4.

Figure 3. *Groeberia pattersoni*, new species. Holotype, M.L.P. No. 68-VI-27-1. Anterior part of skull, left lateral view, photograph and explanatory sketch. "Buccal to M^3" indicates a point on matrix, formerly covered by the zygoma, medial to which is a broken cheek tooth identified as probably M^3. IFO = infraorbital. Mx-Ju = maxillo-jugal. NA = nasal. OR = orbit. Pmx-mx = premaxillo-maxillary. Approximately $\times$ 4.

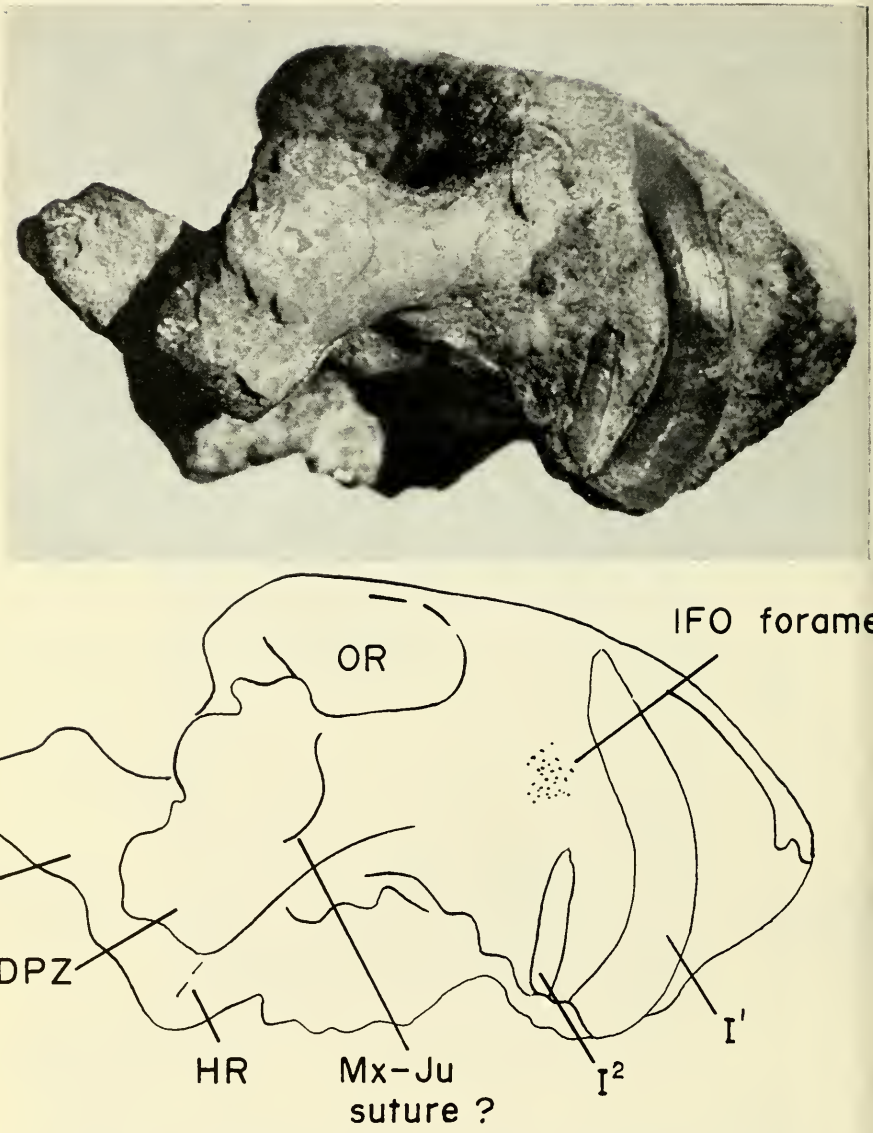


Figure 4. *Groeberia pattersoni*, new species. Holotype. M.L.P. No. 68-VI-27-1. Anterior part of skull, right lateral view, photograph and explanatory sketch. CO = fragment of coronoid process of mandible. DPZ = descending plate of zygoma. HR = fragment of horizontal ramus of mandible. IFO = infraorbital. Mx-Ju = maxillo-jugal. OR = orbit. Approximately × 4.

Figure 5. *Groeberia pattersoni,* new species. Holotype M.L.P. No. 68-VI-27-1. Anterior part of skull. A, dorsal view. B, palatal view. Approximately × 4.

There is a diastema posterior to I^2 and then cheek teeth, but nothing definite can be made out for the latter, except that they are small and brachydont.

The preorbital part of the skull is notably short and deep. In the most probable orientation, it (or the snout) is convex dorsally as a whole and curves downward anteriorly. The nasals are accordingly downcurved and end shortly anterior to I^1. The infraorbital foramen is not definitely visible as the specimen is preserved, but must be of moderate size and in a normal position on the face anteroventral to the orbit and about half way between it and I^2, where there is a depression obscured by matrix on the specimen. On the left side, what is probably part of the premaxillo-maxillary suture is visible just anterior to that depression.

The orbit is rather small and relatively anterior in position, its anterior rim probably in advance of the cheek teeth and certainly well in advance of what is identified as M^3. The stout root of the zygoma below the orbit had an expanded suborbital process or plate, the full extent of which cannot be determined. On both sides, a possible but uncertain maxillo-jugal suture can be seen

Figure 6. *Groeberia pattersoni*, new species. Holotype, M.L.P. No. 68-VI-27-1. Anterior part of skull, anterior view. Approximately × 4.

below the ventral border of the orbit. Posterior to this, and hence on the jugal if the possible suture is such, is a small ventral postorbital process. Uncertainly but probably, there was no dorsal postorbital process, and the orbit was therefore probably open.

The palatal surface is both poorly exposed and poorly preserved, so that little can be made out there with sufficient probability. However, its dorsal (intranasal) surface is partly exposed, and some details can be made out in cross section at the broken posterior surface of the specimen. A palatal vacuity was probably absent or small if present. It appears that the palate between the cheek teeth was deeply arched (concave ventrally). The coronoid process of the mandible can be seen lateral to a posterior tooth, perhaps M^3 or M^4, and lateral to that a section of a deep (vertically) but thin (laterally) zygoma. (See diagram, Fig. 7.)

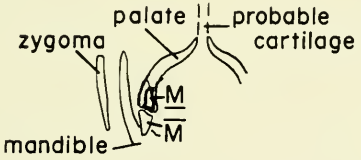


Figure 7. *Groeberia pattersoni*, new species. Holotype, M.L.P. No. 68-VI-27-1. Rough diagram of section at posterior break of specimen as preserved. Not to scale.

Affinities. This specimen adds considerably to data bearing on affinities of the genus, without settling the matter. Patterson's (1952: 3) judgment that *Groeberia* should be distinguished at the family level, as Groeberiidae, is strongly confirmed.

Patterson's evidence that *Groeberia* is a marsupial was in small part positive, largely negative, and partly indirect. The present specimen adds no positive evidence, strengthens the negative evidence, and does not change the indirect evidence. The only really positive evidence from the holotype of *G. minoprioi* for marsupial affinities in general (as distinct from caenolestoid affinities in particular, see below) is the probably inflected angle of the mandible. Even this is not quite certain, because the angle itself is not known, but a crest that would have led to it does decidedly suggest inflection. An inflected angle is strong, but not conclusive, evidence, as a few marsupials do not have the angle inflected and a few placentals do. *G. minoprioi* may have had four

lower molars, and that would again be strong but not fully conclusive evidence, but the possibility that its cheek teeth include one premolar and three molars is not entirely excluded. The known parts of the skull of *G. pattersoni* have no evident features strongly characteristic either of marsupials or of placentals. The absence of palatal vacuities would be more like most placentals, but it is uncertain and there are a number of marsupials without such vacuities.

The negative evidence is that *Groeberia* has no known features that would make reference to the Marsupialia impossible or highly improbable but does have known features that make reference to any other order highly improbable. Here the new specimen confirms and adds somewhat. The habitus is more or less rodent-like, but the two upper incisors are unlike those of any rodent. They are somewhat like those of lagomorphs, but the cheek teeth, even what little can be seen of them in this specimen, definitely rule out pertinence to that group. Limited resemblances of the mandible to those of certain primates, such as the early Cenozoic *Chiromyoides*, as mentioned by Patterson, or the living *Daubentonia*, become even less possibly significant in the light of what is now known of the skull. The skull is unknown in *Chiromyoides*, but its upper incisors are entirely unlike those now known in *Groeberia* and the skulls of other plesiadapids are also quite different (see especially Russell, 1964). There is an interesting resemblance between the short, deep faces of *Daubentonia* and *Groeberia*, but this is quite clearly functionally convergent and the two differ markedly in other respects and in facial details. Almost all other placental orders have basic diagnostic features absent in *Groeberia* or strongly contradicted in this genus.

If *Groeberia* was a placental, it must almost perforce have evolved independently and uniquely from ancestors as primitive and undifferentiated as those now known from the late Cretaceous and, in decreasing numbers and generality, quite early Cenozoic. Here one turns to the indirect and yet cogent evidence: that no such placentals are known from South America; that equally primitive and undifferentiated marsupials are known from there; that those marsupials did diverge in independent and unique lines; and that derivation of *Groeberia* from a potent and definitely South American source is at least a likely hypothesis.

Patterson's views on the affinities of *Groeberia* were buttressed by evidence for referring it to the Caenolestoidea. That evidence,

from the single poorly preserved fragment of mandible then known, was as follows:

1. One greatly enlarged lower incisor, with enamel on anterior face and alveolus (or "parte basal") parallel to median line of symphysis (not to the horizontal ramus or tooth row).
2. Strong salient coronoid process.
3. Molars with short talonids with posterior entoconid and hypoconid, united by a transverse crest, a short *crista obliqua,* and a shallow basin.
4. Molar trigonids with one lingual (probable metaconid) and two labial cusps (probable paraconid and protoconid), as in caenolestoids except Caenolestinae.
5. Trigonids and talonids subequal, as in Palaeothentinae and Abderitinae.
6. Masseteric crest absent; very poorly defined in Palaeothentinae.
7. Inflection of lower border beginning anterior to cheek teeth; usually posterior to cheek teeth in Caenolestoidea but beneath M_4 in *Parabderites bicrispatus.*

This was a valid analysis of the admittedly deficient evidence, but the conclusion may be retroactively queried in the light of present knowledge. As to (1), no unquestioned caenolestoids have hypselodont incisors comparable to these in form or function, but the placing of the alveoli is an interesting point. (2) is not particularly diagnostic. Regarding (3)–(5), the molar structure is difficult to make out on the specimen, but I believe that Patterson has correctly interpreted it. However, it differs characteristically from probably ancestral didelphid structure in little more than the more labial position of the paraconid, an occlusal adjustment that could well arise more than once. (6) is somewhat dubious and is not diagnostic for caenolestoids. (7) differs from caenolestoids more than it resembles them.

A reasonable but inconclusive case was presented on the basis then available and pending acquisition of further knowledge. The still quite limited further knowledge now acquired does not flatly contradict that case, but neither does it strengthen it, and it even weakens it to some extent. I see no special resemblance of known parts of *G. pattersoni* to any unquestionable caenolestoid. On the contrary, the extreme abbreviation of the face, the reduction of the incisors to two, and their truly gliriform, hypselodont nature

are almost the opposite of known trends in the Caenolestoidea. Even the Polydolopidae, superficially most seemingly rodentlike of undoubted caenolestoids, are not really very rodentlike in habitus and evolved in a direction very unlike that of *Groeberia* (see especially Simpson, 1948; Paula Couto, 1952).

Patterson (1952: 6) also compared *Groeberia* with *Argyrolagus* and concluded that they are not specially related beyond their both being marsupials. With greatly increased information on *Argyrolagus,* I agreed (Simpson, 1970), and the present addition to knowledge of *Groeberia* does not change that opinion. Indeed, the contrasts between *Argyrolagus* and *Groeberia,* both somewhat rodentlike, are remarkable. *Argyrolagus* has an extremely elongate, shallow rostrum and face, very posterior orbit, short, shallow zygoma, hypselodont cheek teeth. *Groeberia* has extremely short, deep rostrum and face, very anterior orbit, long deep zygoma, brachydont cheek teeth.

Almost complete knowledge of dentition and skeleton of *Argyrolagus* contradicted previous opinion that it might be a caenolestoid and required placing it in a separate superfamily. I suspect that the same might happen if we had equally good information on *Groeberia,* but we do not. This knowledge is still so scanty that I believe it would be unreasonable or, at best, premature at this point to classify the Groeberiidae other than as Marsupialia *incertae sedis.*

Proposals have long been made to divide the marsupials into suborders, and recently, to divide them into two or more orders. If suborders Polydactyla and Syndactyla were recognized, I would predict that discovery of foot bones would aline *Groeberia* with the polydactyls. If Polyprotodonta and Diprotodonta were recognized, *Groeberia* would be descriptively, typologically, or phenetically diprotodont, but I believe that would be profoundly misleading because it inevitably suggests connection with the Australian diprotodonts, and *Groeberia* is not so *incertae sedis* as all that. It has no suggestion at all of Australian affinities. The ordinal system of Ride (1964) has no sure ordinal place for it, as the evidence that it may be a "paucituberculate" (caenolestoid) is insufficient, but reference to the Marsupicarnivora would be rather anomalous (although like all marsupials it doubtless arose from the group so named by Ride), and pertinence to the Peramelina or Diprotodonta (*sensu* Ride) is out of the question. Kirsch's (1968) arrangement also has no sufficiently likely place for *Groeberia* in any one of his orders.

Biology. In the absence of postcranial remains, nothing can be safely inferred as to body build, limb proportions, or locomotion in *Groeberia.* Biological inferences are further limited by the absence of specimens of the neurocranium and by the imperfections of the only two specimens known. The following are the principal characters of probable functional importance that are known:

1. Face and snout short.
2. Face and mandible deep.
3. Infraorbital foramen small.
4. Orbit relatively anterior.
5. Orbit of moderate size.
6. Masseteric origin on zygoma.
7. Heavy hypselodont incisors with labial enamel.
8. I^1 recumbent.
9. Short lower diastema near alveolar level.
10. Comparatively small, brachydont cheek teeth.
11. Large coronoid process.
12. Small (no?) masseteric crest.
13. Inverted angle.

The habitus is rodentlike at first sight, but no living rodent and in fact no other animal, living or fossil, known to me combines all those characteristics. 3, 6, 11, and 13 are usual and 4, 5, and 10 common in marsupials; all but 13 are also fairly common in placentals. 1, 2, 7 and 8 occur in the other known marsupials that are most rodentlike, the Australian wombats. They are lacking in caenolestoids, also somewhat but much less rodentlike in some genera. With only the partial exception of 13, all these characters occur in one placental rodent or another, but not in this combination. For example some caviomorphs, such as *Echimys,* have characters 5, 7, 8, 10 and a functional modification of 13, but notably differ in 3, 6, 9, 11 and 12. *Aplodontia* has 3, 4, 6, 7, moderate 8, 11 and moderate 12, but differs markedly in 1, 2, 5, 9, 10, and 13. *Xerus* (a sciurid) agrees well in 1, 3, 4, 7, 8, and 10, but less well in 2 and 9, and not at all in 5, 6, 11, 12, and 13.

There is no doubt that *Groeberia* was a powerful gnawer, at least as much so as hares, rodents, wombats, or *Daubentonia.* Its incisors were not merely a pincer apparatus as in all known caenolestoids and all diprotodonts (phalangeroids) except the wombats. They are decidedly more adapted to gnawing than in the argyrolagoids, even though the latter, unlike caenolestoids, also have

hypselodont incisors. Gnawing is strongly connected with food gathering in recent animals, but not exclusively so. On the other hand, *Groeberia's* small area of brachydont cheek teeth is very different from the hypselodont teeth of wombats, argyrolagoids, and many rodents, and is more nearly comparable with the cheek dentition of caenolestoids, squirrels, and *Daubentonia.* The combination suggests a food obtained by gnawing but prepared for deglutition by crushing or comminution without grinding. Possibilities are bark or wood-boring insects or fruits or nuts with hard shells. However, some murids with strong gnawing apparatus and limited, brachydont cheek teeth are virtually omnivorous or even carnivorous. I see no way to correlate *Groeberia's* unique combination of characters with an equally unique diet or with any closely specific way of life.

No rodents are known in the Divisadero Largo or any earlier South American formation. Simpson, Minoprio, and Patterson (1962: 289) mentioned the possibility that the presence of the rodentlike marsupial *Groeberia* indicated age before rodents reached that area, hence pre-Deseadan. The ecological aspect of that suggestion would still hold even if the determination of the relative time of entry of rodents proved to be incorrect. (There is still no opposing evidence.) The rodent habitus surely evolved elsewhere and was in being when the first rodents entered South America, whether in the Deseadan or, as is quite likely, somewhat earlier. On the other hand, the ancestral habitus of *Groeberia* almost certainly evolved in South America before rodents reached there, convergent to some extent toward the absent rodents and entering niches with some points of similarity.

Zoogeography. It is the most reasonable hypothesis that the Groeberidae did evolve in South America, even though their possible relationship to the Caenolestoidea is quite dubious, and there is no suggestion of special descendant relationship (involving specialization) to any other South American group. Origin from South American didelphoids is as likely as any other, if not more so. There is no special resemblance to any Australian marsupials suggestive of genetic affinity beyond the remote ancestry of all marsupials. No marsupials are known from Africa and any idea of connection there would be purely gratuitous at present.

Nevertheless it is strange that three of the most peculiar, most specialized known groups of South American marsupials appear in the presently available record without known ancestors, only to

vanish again immediately (geologically speaking) or soon thereafter: Groeberiidae, only in the Divisadero Largo formation; Necrolestidae, only in the Santa Cruz formation; and Argyrolagidae, only from Huayquerian to Uquian. A possible clue is that all these faunas are in Temperate Zone Argentina and that earlier faunas are as yet very inadequately known farther north on the continent. It is a reasonable hypothesis, as yet without direct evidence, that these groups evolved in what are now (and quite likely were then) the tropics and are picked up in our record only when they spread rather briefly to what was for them a marginal area.

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B R E V I O R A

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NON-SPECIFICITY OF HOST-SELECTION IN THE ECTOPARASITIC SNAIL *ODOSTOMIA (MENESTHO) BISUTURALIS* (SAY) (GASTROPODA: PYRAMIDELLIDAE)

Robert C. Bullock and Kenneth J. Boss

ABSTRACT. Ectoparasitic pyramidellid gastropods have often been considered host-specific, although a few species have been reported to feed on a variety of hosts under laboratory conditions. A large population of *Odostomia (Menestho) bisuturalis* (Say) at Duxbury Beach, Massachusetts, provided an ideal opportunity to study the association of this ectoparasite with the various mollusks found in the vicinity. Our results revealed that *O. bisuturalis* was associated with seven species of mollusks, most commonly *Nassarius obsoletus* (Say) and *Mytilus edulis* Linnaeus. The great abundance of *O. bisuturalis* and the fact that *Crassostrea virginica* (Gmelin), its usual natural host, was absent from the study area, appear to account for the non-host-specificity observed.

INTRODUCTION

The host-specificity of the ectoparasitic snails of the family Pyramidellidae has been the subject of several papers during the last decade. Early observations led some workers, notably Fretter and Graham (1949; 1962), to state that these ectoparasites were host-specific. More recent studies have revealed that under laboratory conditions certain pyramidellids actually feed on a variety of hosts (Ankel and Christensen, 1963; Scheltema, 1965; Robertson, personal communication), although possible host-preference may be a factor (Boss and Merrill, 1965). The observations reported here suggest that some species of pyramidellids are not host-specific.

What actually constitutes a true parasitic relationship has been questioned (Robertson and Orr, 1961; Dehlinger, unpublished MS). While observations of pyramidellids associated with

various organisms indicate, by their proximity or physical contact, possible parasite-host relationships, most authors have been wary of such evidence. Robertson (personal communication) stated that the presence of an *Odostomia* on a possible host may only reflect the pyramidellid's need for a suitable substrate. This view is supported by some of our observations and those of Scheltema (1965), who noted *O. bisuturalis* clinging to the under surfaces of stones in a region where *Littorina littorea* L., a "laboratory host" for this species, was abundant. Recent workers have indicated what constitutes a true parasitic relationship: insertion of the proboscis and action of the buccal pump (Robertson, personal communication; Scheltema, 1965) or when the parasite is "less than ⅛ in. from the edge of the mantle of the host" (Boss and Merrill, 1965). Although the former is a more exact method, we have necessarily followed Boss and Merrill (1965), since our observations were made during the low tide period when the ectoparasites were not actively feeding on exposed hosts.

OBSERVATIONS

An abundance of *Odostomia* (*Menestho*) *bisuturalis* (Say, 1822) was noted on the tidal flat on the harbor side of Duxbury Beach, Massachusetts, in June, 1969. Sampling at several stations along the beach during a -1.6 tide on 3 June and subsequent visits to the study area provided ample field evidence of the occurrence of this snail on numerous intertidal molluscan hosts.

The *Odostomia* were not limited to a particular region of the tidal flat, for they were found from below the low-water mark to the upper portion of the intertidal zone. Quantitative samples were taken in the region at the east end of the Duxbury Beach bridge. All mollusks collected were carefully examined for the presence of *Odostomia*. *O. bisuturalis,* the only pyramidellid found, was collected from seven different species of mollusks: *Littorina littorea* (L.), *Urosalpinx cinereus* (Say), *Crepidula convexa* Say, *Crepidula fornicata* (L.), *Nassarius obsoletus* (Say), *Nassarius trivittatus* (Say), and *Mytilus edulis* Linnaeus. They were also observed on the egg capsules of *Nassarius* sp. and *Polinices* sp., and on empty shells.

O. bisuturalis was most abundant on three hosts: *Mytilus edulis,* which formed large mats on the mud flats, and on the snails *Nassarius obsoletus* and *Littorina littorea,* which occasionally had

from one to three ectoparasites on the operculum or on the lip of the shell. The *Mytilus* that were observed in water often had a number of ectoparasites situated on the margins of the mantle, away from the hinge, similar to the position assumed in *Odostomia scalaris* MacGillivray on *Mytilus* in Europe. However, most of the *Mytilus* population at Duxbury was exposed at low tide and the ectoparasites had migrated to moist areas within the *Mytilus* mat. In the laboratory we have observed *O. bisuturalis* feeding on *Mytilus*.

Table I shows the relative abundance of *Odostomia* on three hosts. In the case of *Nassarius obsoletus* several items should be noted: 1) the parasites occurred on samples with a large mean length in a frequency of one *Odostomia* to three or four *Nassarius;* 2) smaller individuals of *Nassarius* were significantly less parasitized, with only one parasite per ten individuals. This latter observation was also noted in studies of *O. impressa* (Say) (Hopkins, 1956) and *O. dianthophila* Wells and Wells (Wells and Wells, 1961). At one station *N. obsoletus* was present in large numbers, possibly 12,000/m^2, with an equally high concentration of *O. bisuturalis,* 7,000/m^2. These figures indicate that at times *O. bisuturalis,* a usually overlooked organism, must play a moderately significant role in the flow of energy in a tidal flat community. In other species, not quantitatively sampled, the occurrence of *Odostomia* was even greater, in some cases amounting to two ectoparasites per host, e.g., *Littorina*.

Previous published records of field observations have not revealed *O. bisuturalis* in association with any of the seven species of mollusks reported in this study. In the laboratory, *O. bisuturalis* is known to feed on: *Littorina littorea* (L.) (Scheltema, 1965; Robertson, 1967); *Bittium alternatum* (Say) (Scheltema, 1965); *Crucibulum striatum* (Say) and *Crepidula fornicata* (L.) (Boss and Merrill, 1965). Previously, the only known natural host of *O. bisuturalis* was the American oyster, *Crassostrea virginica* (Gmelin) (Loosanoff, 1956; Boss and Merrill, 1965), a species not present at Duxbury Beach.

DISCUSSION

These observations demonstrate that at least one pyramidellid is not host-specific. Further, laboratory studies have shown that certain *Odostomia* may have numerous hosts. Thus, should these

species actually be non-host-specific, as *O. bisuturalis* seems to be, an examination of all environmental factors involved in host-specificity and host-preference becomes imperative.

The great abundance of *O. bisuturalis* led to the consideration of the question of density-dependent factors in feeding behaviour. While our observations show the non-specific host-selection of *O. bisuturalis,* they do not reveal any specific information concerning host-preference. An abnormally large population of *O. bisuturalis* or a diminished preferred food source might force many individuals to feed on hosts they would otherwise reject.

The biological relationship between a motile ectoparasite and host-species can be likened to that between a predator and its prey. The odostomia-type of predator-prey relationship with respect to food preference is commonly observed in animals not totally dependent on one organism for survival. It has been demonstrated that total food abundance, relative abundance of food types, spatial distribution of foods and predator satiation affect feeding preferences in some animals (Ivlev, 1961). In mollusks, for example, Wells (1958) found that although the opportunistic gastropod *Fasciolaria hunteria* (Perry) prefers to eat the small oyster drill, *Urosalpinx,* it will eat oysters if only a minimal number of the more desirable gastropods are present. Further, in a study of the relationship between time and energy in food preferences, Emlen (1966: 617) suggested that: 1) "Animals should be more selective in their choice of foods when satiated or when food is common, more indiscriminate when starved or when food is scarce"; and, 2) "Food preferences appear to change readily and appropriately to changes in the environment."

The particular circumstances in which the ectoparasitic population existed were unusual in that: 1) there was a very large population of ectoparasites; and, 2) the preferred natural host for this species, *Crassostrea virginica,* was not present in the local ecosystem. Thus, our observations corroborate the hypotheses of Emlen and indicate that *Odostomia bisuturalis* may have various host-species under natural conditions.

ACKNOWLEDGMENTS

The manuscript was critically read by Messrs. R. I. Johnson and M. K. Jacobson and Dr. R. D. Turner. Mr. W. Baranowski brought our attention to the occurrence of great numbers of *Odostomia* at the Duxbury site, and Mr. S. Britz measured the specimens.

TABLE 1.
Occurrence of *Odostomia bisuturalis* on Hosts at Duxbury Beach, Massachusetts, in June, 1969

Host	Size of sample hosts/parasites	Sampled area (m^2)	Total hosts/(m^2)	Total parasites/(m^2)	Ratio parasites/host	Length range of hosts (mm)	Mean length of hosts (mm)	Length range of parasites (mm)	Mean length of parasites (mm)
N. obsoletus	44/16	1/4	176	64	.360	6.9-20.3	15.85	1.84-3.36	2.61
	97/55	1/128	12416	7040	.567	11.1-20.8	15.46	1.84-4.08	2.81
	235/21	1/4	940	84	.089	4.5-20.0	9.53	1.92-3.60	2.56
	84/25	1/4	336	100	.297	5.7-19.5	16.02	1.92-4.24	2.59
L. littorea	27/42				1.55	15.0-23.3	18.27	1.12-3.84	2.32
	2/4				2	11.8-17.1	14.45	2.00-2.72	2.50
U. cinereus	12/13				1.08	3.6-26.8	20.12	1.52-3.52	2.42

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BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. 8 JANUARY, 1971 NUMBER 364

A NEW SCINCID LIZARD FROM BOUGAINVILLE, SOLOMON ISLANDS

Allen E. Greer and Fred Parker[1]

ABSTRACT. The relationships of *Sphenomorphus transversus,* n. sp., from Bougainville, Solomon Islands, are obscure, but in squamation it is most similar to *maculatus, boulengeri, formosensis, lineopunctulatus,* and *indicus* from eastern Asia; *melanochlorus* from New Guinea; and *sanctus* from Sumatra and Java. *S. transversus* differs most noticeably from these species and from other Bougainville skinks in its dorsal pattern of transverse dark brown bands on a light olive ground color.

During investigations in 1960–1963 by Parker on Bougainville, Solomon Islands, a single individual of a previously undescribed species of skink was collected. Since one subsequent trip (1966) has failed to uncover other specimens of the species, and as the possibilities of a second return trip to Bougainville in the near future are slim, it seems best to describe the new species from the single specimen at hand.

On the basis of current generic concepts, the species is assigned to the genus *Sphenomorphus* and may be known as

Sphenomorphus transversus[2] new species

Holotype. Museum of Comparative Zoology 76485; collected by a native for Fred Parker at about 2000 feet above sea level in an area approximately five miles east of Kunua, northeastern Bougainville (Fig. 1), on 9 September 1962.

[1] P. O. Box 52, Daru, Western District, Territory of Papua and New Guinea.

[2] The species name calls attention to the dark transverse bars on the dorsum.

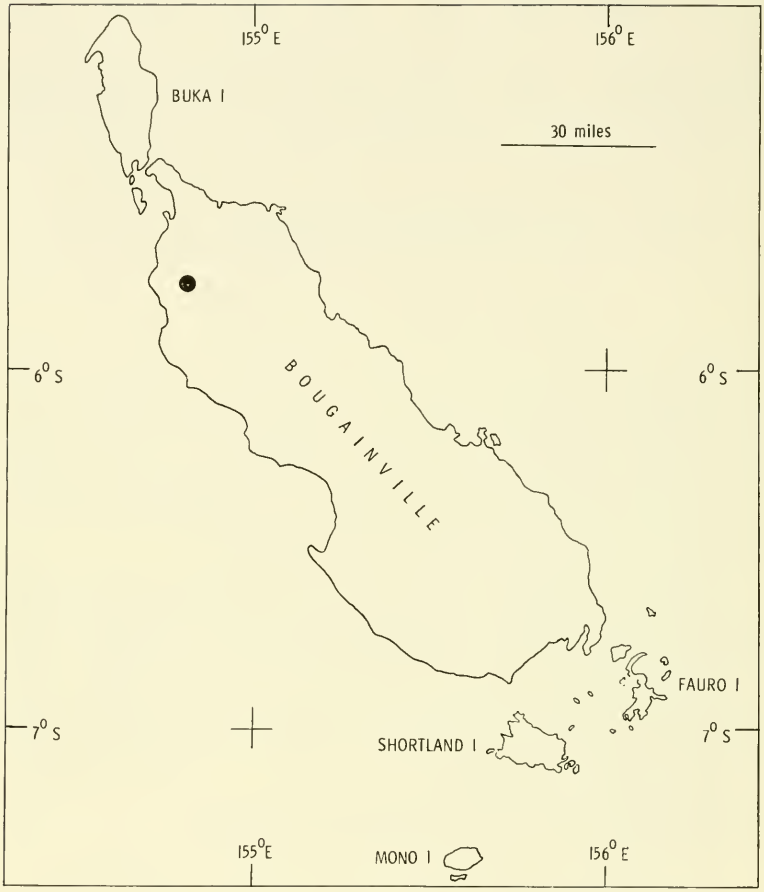

Figure 1. Map of Bougainville showing the location approximately 5 miles east of Kunua where the type and only known specimen of *Sphenomorphus transversus* was collected.

Diagnosis. Similar in squamation to those skinks of the genus *Sphenomorphus* (Table 1) that have a single anterior loreal, the frontal in contact with 3 or more of the 5 or more supraoculars, frontoparietals and interparietal distinct, no nuchals or transversely enlarged scales in the two vertebral rows (Figs. 2 and 3),

and the digits and limbs well developed and overlapping when adpressed to the body, but differing from other skinks with this diagnosis in having the following combination of characters: prefrontals separated medially, 36 rows of smooth scales around midbody, 28–29 smooth subdigital lamellae on the 4th toe, and a color pattern of brown transverse bands on a light olive-green ground color (Figs. 4 and 5) — a color pattern most similar to those of the distantly related *Sphenomorphus flavipes, Scincella prehensicauda,* and *Leiolopisma semoni* of New Guinea.

Description. Body form relatively slender; well-developed pentadactyl digits and limbs that overlap when adpressed to the body (tip of 4th toe reaches middle of forearm); snout-vent length 68 mm, tail 92 mm.

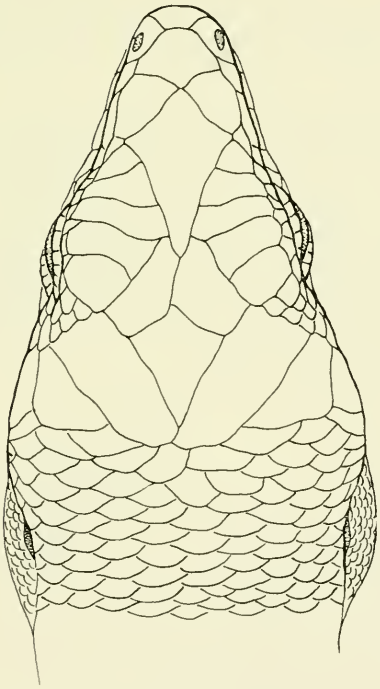

Figure 2. Dorsal view of the head of the holotype of *Sphenomorphus transversus* (MCZ 76485).

Head not depressed, snout somewhat pointed; rostral slightly wider than deep, projecting slightly onto dorsal surface of snout between nasals; external naris in single nasal; no supranasals; single anterior and posterior loreals; frontonasal slightly wider than long, forming a short suture with the rostral and a very short suture with the frontal; prefrontals large, barely separated at their inner angles; frontal 1¾ times as long as wide, in contact with the three anteriormost supraoculars; 5 supraoculars, the first smallest, but in no way to be confused with the anterior superciliaries; lower eyelid scaly; 6th supralabial most directly below eye; a complete row of subocular scales separates scales of lower eyelid from supralabial series; frontoparietals paired and subequal in size with the single interparietal that is sharply pointed posteriorly; parietals meeting behind interparietal and bordered posteriorly by a single large temporal on either side and 5 large dorsal scales between the temporals; no symmetrical series of nuchals.

External ear opening vertically elliptic, without auricular lobes; tympanum sunk slightly below level of skin; 36 smooth scales around midbody, the scales of the two vertebral rows not larger than those of the immediately adjacent rows; a pair of enlarged preanals; scales of three median subcaudal rows subequal in size.

Digits rather long and slender; subdigital lamellae smooth and undilated throughout length of digit; 28–29 lamellae beneath 4th (longest) toe; upper surface of 4th toe covered by one or two

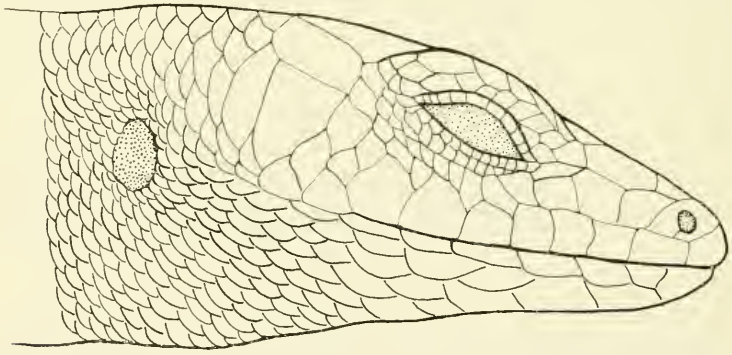

Figure 3. Lateral view of head of *Sphenomorphus transversus* (holotype).

single scales at distal end, 3 rows of scales throughout center part and 4 rows near base (see Brongersma, 1942).

Dorsal ground color light olive with a series of complete and incomplete transverse dark brown bands from nape to base of tail, the brown bands terminating in slightly expanded blotches on sides (Fig. 5), an effect especially pronounced at midbody; a horizontal brown stripe from anterior loreal through eye to temporal region; brown blotches on anterior and upper surfaces of limbs as well as on upper surface of tail; venter immaculate except for a few faint brown spots on throat and underside of tail.

In life the undersides of the limbs, body, and tail were bright yellow.

Field Notes. The only known specimen of *S. transversus* was taken by a native collector under a decaying log on the steep side of a montane river valley covered with tall primary forest. The natives did not recognize it as being distinct from *S. concinnatus*, a species common at the type locality of *S. transversus*.

Morphological Comparisons with Other Bougainville Skinks. S. transversus is immediately distinguishable from *S. concinnatus* by its more sharply tapered, longer snout; the absence of a dark blotch between the ear opening and the forelimb; the smaller external ear opening; and, the regular transverse barring.

Only two other Bougainville skinks, *S. taylori* and *S. cranei*—both very different from *S. transversus* in squamation — have transverse bands on the dorsum. In both these species, however, the dorsal pattern consists of very light transverse bands on a dark ground color, whereas in *S. transversus* the transverse bands are darker than the ground color. *S. transversus* also has a more noticeably pointed snout than either *S. taylori* or *S. cranei.*

Skull Characters. It is extremely difficult, if not impossible, to remove the skull of most skinks without severely damaging the skin of the head. For this reason we have not attempted to prepare a skull from the type and only known specimen of *S. transversus.* We have, however, had a palatal view of the skull, and the salient features are as follows: there are 9 premaxillary teeth; the palatine and pterygoid bones meet along the midline to form a fairly extensive secondary palate; there is no ectopterygoid process; and, there are no pterygoid teeth. Unfortunately, these characteristics are not particularly diagnostic, for they would not exclude *S. transversus* from close relationship with any number

of other lygosomines, including those discussed below that are most like *S. transversus* on the basis of external morphology.

Comparison with Morphologically Similar Species. In squamation *S. transversus* is most similar to those species of *Sphenomorphus* (Table 1) that have a single anterior loreal, the frontal in contact with 3 or more of the 5 or more supraoculars, the frontoparietals and interparietal distinct, no nuchals or transversely enlarged scales in the two vertebral rows, and the digits and limbs well developed and generally overlapping when adpressed to the body. This assemblage, which is almost surely not monophyletic, is distributed from southern Asia through the Indo-Australian archipelago and Philippines to New Guinea, but not Australia.

Seven species in this group have the prefrontals separated medially (in all or some individuals), as is the case in the single specimen of *S. transversus*. Six of these seven species (*maculatus, boulengeri, formosensis, lineopunctulatus,* and *indicus* from southern Asia and *melanochlorus* from New Guinea) have substantially fewer subdigital lamellae on the 4th toe (16–22) than does *transversus* (28–29), and the seventh (*sanctus* from Sumatra and Java) has finely striated body scales to distinguish it from the smooth-scaled *transversus*. Furthermore, none of these seven species have a dorsal body pattern consisting of well-defined dark crossbars as does *transversus*.

This very characteristic dorsal body pattern of dark crossbars on a light ground color is most similar to the patterns of the crossbanded color morph of *Sphenomorphus flavipes,* the females of *Scincella prehensicauda,* and of all *Leiolopisma semoni.* These three species are endemic to neighboring New Guinea and might, therefore, seem to be likely relatives of *Sphenomorphus transversus*. Current work on scale and palatal characters, however, indicates that while *flavipes, prehensicauda* and *semoni* are themselves closely related (in spite of current generic allocations), they are only distantly related to *Sphenomorphus transversus*.

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Dr. Ernest E. Williams of the Museum of Comparative Zoology read the manuscript in several drafts and offered several helpful suggestions. Mr. Laszlo Meszoly did the drawings for Figures 2 and 3, and Mr. Ian T. Riddell took the photographs for Figures

4 and 5. Part of Greer's work on this paper was done while he was a postdoctoral fellow of the National Science Foundation. Partial support was provided by National Science Foundation grant GB 6944 to Ernest E. Williams.

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TABLE 1

Species most similar to *Sphenomorphus transversus* in squamation. Species which we have examined are marked with an asterisk (*). In those instances in which no reliable data on meristic characters have been available in the literature only data from the type description are given.

Species	*Author*	*Range*	*Scales around midbody*	*Subdigital lamellae on 4th toe*	*Adpressed limbs meet*	*Prefrontals meet*	*Number of supraoculars (touching frontal)*	*Nuchal pairs*
*florense**	Weber, 1890/91	Flores Island	44-50	27-29	+	+	6-7 (4)	—
kühnei	Roux, 1910	Kei Islands	42	34	+	+	7 (4)	—
misolense	Vogt, 1928	Misol Island	42	22	+	+	7 (3)	—
*arborens**	Taylor, 1917	Philippines	40-42	21	+	+	5 (3)	—
*maculatus**	Blyth, 1853	SE Asia	38-42	16-22	+	—	5 (2-3)	—
*striolatus**	Weber, 1890/91	Flores Island	40	26	+	+	7 (4)	—
dussumieri	Duméril & Bibron, 1839	SW India	40	20-25	+	+	4-5 (2-3)	—
*boulengeri**	Van Denburgh, 1912	Formosa, Hainan, SE China	36-40	18-20	+	+ or —	4 (2-3)	—
*formosensis**	Van Denburgh, 1912	Formosa, SE China	32-38	16-20	+	+ or —	4 (2-3)	—

lineopunctulatus	Taylor, 1962	Thailand	38	22	+	−	4 (3)	−
*indicus**	Gray, 1853	Southern Asia	30-38	16-22	+	+ or −	6 (2-3)	−
melanochlorus	Vogt, 1932	New Guinea	36	21	+	−	5 (3)	−
*transversus**	new species	Bougainville	36	28-29	+	−	5 (3)	−
*aignanus**	Boulenger, 1898	St. Aignan I.	32-36	40-42	+	+	5 (3)	−
*sanctus**	Duméril & Bibron, 1839	Sumatra and Java	32-34	25-30	+	−	5 (3)	−
milnense	Boulenger, 1903	New Guinea	30-32	35-37	+	+	5 (3)	−

Figure 4. Dorsal view of the holotype of *Sphenomorphus transversus* (MCZ 76485) showing the dark transverse bands which give the species its name.

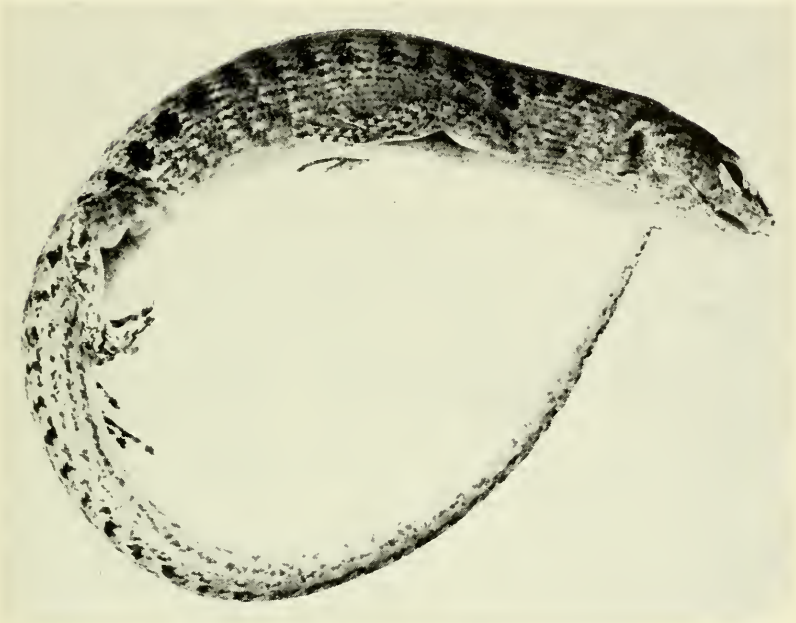

Figure 5. Lateral view of *Sphenomorphus transversus* (holotype).

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. 15 JANUARY, 1971 NUMBER 365

CHARACTERS AND SYNONYMIES AMONG THE GENERA OF ANTS. PART IV. SOME GENERA OF SUBFAMILY MYRMICINAE (HYMENOPTERA: FORMICIDAE)

William L. Brown, Jr.[1]

ABSTRACT. *Archaeomyrmex* is a new junior synonym of *Myrmecina*, and tribe *Archaeomyrmicini* accordingly is a synonym of *Myrmecinini*. *Dodous* is a new junior synonym of *Pristomyrmex*, and the synonymy of *Hylidris* under *Pristomyrmex* is reaffirmed. *Limnomyrmex* is a new junior synonym of *Leptothorax* subgenus *Nesomyrmex*.

The genera considered in this part all belong to subfamily Myrmicinae. My main purpose here is to explain briefly why some new synonymy should be proposed. The taxa concerned have all been studied during the course of the project "a reclassification of the Formicidae," supported by National Science Foundation Grants G-23680, GB-2175, and GB-5574. The taxonomic conclusions will eventually be embodied in a synopsis and illustrated keys to the ant genera of the world. I feel that justification for revisionary changes should be published as the need for the changes becomes clear. In this way, important findings of the study are made available for use by all ant taxonomists without undue delay, and the synoptic parts can be freed from the clutter of many detailed taxonomic arguments.

Myrmecina

Myrmecina Curtis, 1829, Brit. Entom. 6: 226, pl. 265, male. Type species by original designation *Myrmecina latreillii* = *Formica graminicola*.

Archaeomyrmex Mann, 1921: 448-451. Type species: *Archaeomyrmex cacabau*, by original designation. NEW SYNONYMY.

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The unique type of *A. cacabau* has been searched for in vain in the U. S. National Museum and Museum of Comparative Zoology ant collections, and must be considered lost. Fortunately, Mann's description and figures are reasonably detailed. From them, it is clear that the species is essentially a *Myrmecina,* a fact acknowledged by Mann when he wrote: "The epinotal and petiolar structure are not unlike certain species of *Myrmecina.*" Mann emphasized the ventrolateral carina on each side of the head, probably without realizing that this is an invariable character of *Myrmecina.* He also cited the partly smooth, partly costate sculpture of the body, especially the trunk, which does set this species off from the "average" *Myrmecina.* But *Myrmecina* forms with more or less of the head and trunk smooth have not been completely unknown, and they even occur as phenetic variants in species that are usually heavily sculptured in these regions.

Several *Myrmecina* species (at least three of them still undescribed) with predominantly smooth and shining head and trunk are in the MCZ collection. Two of the undescribed species are from the New Hebrides; in each of these, the posterior pair of propodeal teeth is spiniform, but the coarse costate sculpture of the lower pleural areas is preserved, as it is in *cacabau.* Another smooth species has come to me from the Philippines. The geographical and morphological gaps are thus closed between the Fijian and Indo-Australian representatives of what is obviously a single stock. A complete examination of the *A. cacabau* description fails to reveal any character that will separate it from *Myrmecina* at generic level. Together with the two New Hebrides species, *cacabau* should be taken to represent no more than a weak species-group of *Myrmecina.*

Incidentally, an interesting characteristic of some of these species is the extreme reduction of antennomere III, just distal to the pedicel. The distinction between "11-segmented" and "12-segmented" antennae in these forms may prove impossible to maintain as a key character.

Mann's tribe ARCHAEOMYRMECINI of course falls as a **new synonym** of Myrmecinini.

Pristomyrmex

Pristomyrmex Mayr, 1866: 903. Type species: *Pristomyrmex pungens,* monobasic.

Hylidris Weber, 1941: 190. Type species: *Hylidris myersi,* by original designation. — 1952: 15-22. Synonymized by Brown, 1953: 9-10.

Dodous Donisthorpe, 1946: 145; worker, male, larva. Type species: *Dodous trispinosus,* by original designation. NEW SYNONYMY.

Dodous was based on the single species *trispinosus,* from Cocotte Mountain, Mauritius. Syntypes of this species deposited in the British Museum and in the Museum of Comparative Zoology are basically *Pristomyrmex* in form, but they have an extra pair of small teeth on the mesonotum, and the head and trunk are finely and regularly costulate (= striate). The larva, rather vaguely figured in the original description (fig. 4), has the elongate, protuberant head characteristic of *Myrmecina* and *Pristomyrmex.* Donisthorpe also figured the male, which is like known *Pristomyrmex* males in general habitus. The genitalia as very briefly described may be aberrant, but then the genitalia have not been studied at all in most other *Pristomyrmex* species.

A second species of *Dodous, D. bispinosus,* was described from Mauritius by Donisthorpe in 1949. I collected a small sample of strays of this species at the type locality, Le Pouce (Mountain) on 1 April 1969, the last day of a short stay on Mauritius. The specimens were all foraging workers taken on trees and on the main path through the scrubby native forest at about 800 m elevation on the "plateau" near the summit. (A sudden storm prevented my finding any nests.) *D. bispinosus* differs from *D. trispinosus* in lacking the mesonotal teeth (though actually some of my *bispinosus* specimens have low mesonotal tubercles in place of the teeth) and in having predominantly smooth and shining sculpture. In fact, *D. bispinosus* is a rather ordinary, if slightly long-legged, *Pristomyrmex,* and *D. trispinosus* goes only one step beyond. It seems absurd to put these two closely related species in different genera. Discovery of the annectant *D. bispinosus* makes it clear to me that *Dodous* is only the Mauritian complement of the widespread Old World genus *Pristomyrmex.* The concept of *Dodous* as a separate genus is, as far as I am concerned, as dead as its namesake.

I have already (Brown, *loc. cit.*) placed Weber's *Hylidris* as a synonym of *Pristomyrmex.* Weber opposed this synonymy, maintaining that *Hylidris* is a distinct genus. But when he described *Hylidris,* Weber took no note of the African species of *Pristomyrmex* described previously by Santschi, Arnold, and Karavaiev, at least some of which are senior synonyms of his own *Hylidris* species and

subspecies (Weber, 1952). Weber has never produced a characterization of *Hylidris* that will separate it as a genus from *Pristomyrmex,* and particularly from the long-synonymized "subgenus" *Odontomyrmex.* I have collected *P. orbiceps* in the Ivory Coast, and can affirm that colony behavior (lethisimulation), larval form, and general adult morphology are fully those of Asian and Australian *Pristomyrmex* as I have seen them in nature.

Pristomyrmex is a sharply defined and compact genus, and there is no reason that I know of to set the African species apart from it. In fact, the African species are as nearly "average" for the genus *Pristomyrmex* as one is likely to find.

Some other misconceptions explicit or implied in Weber's discussion of 1952 need correction. The petiole of *Pristomyrmex* has a distinct anterior peduncle, though it is short in some species. In contrast, the related genus *Myrmecina* has a sessile petiole of more or less prismatic shape. *Pristomyrmex* and *Myrmecina* are not very closely related to tribe Tetramoriini, though two species have been wrongly placed in tetramoriine genera in the past. The larvae, for one thing, are very different, and it seems that they may furnish the best tribal character for the Myrmecinini if we limit the tribe to *Pristomyrmex, Myrmecina, Acanthomyrmex,* and possibly the little-known *Perissomyrmex* of Guatemala, the larvae of which have not yet been found. Tribe Tetramoriini is not "worldwide" in distribution, if one ignores obvious introductions by man. The tribe has no native species in South or Central America, and only a single species of *Xiphomyrmex* occurs in (Sonoran) North America.

Leptothorax subgenus *Nesomyrmex*

Nesomyrmex Wheeler, 1910, Bull. Amer. Mus. Nat. Hist., 28: 259. Type species *Nesomyrmex clavipilis,* monobasic.

Leptothorax (Goniothorax) auct., preoccupied.

Leptothorax (Caulomyrma) Forel, 1914, Bull. Soc. Vaudoise Sci. Nat., 50: 233.

Limnomyrmex Arnold, 1948, Occas. Pap. Nat. Mus. S. Rhodesia, 2(14): 222. — 1952, *Ibid.,* 2(17): 460, discussion. Type species *Limnomyrmex straminens,* monobasic. NEW SYNONYMY.

Soon after its description, the late Dr. Arnold and I engaged in correspondence on the question of the distinctness of *Limnomyrmex* from the subgenus *Nesomyrmex* of *Leptothorax.* He stoutly maintained that *Limnomyrmex* was a good genus, and in 1952 (*loc. cit.*) he argued again in print for this stand. Now that I have finally

seen the unique worker type of *L. stramineus* in the Arnold Collection at Bulawayo, I can only place this species among the other known African *Nesomyrmex*. I have searched in vain for any characters that might set *Limnomyrmex* apart as a genus. In the form of the trunk and both petiolar and postpetiolar nodes, it is about "average" for a *Nesomyrmex* from Africa, and resembles in a subdued way some neotropical members of the group. Sculptural and a few other differences mark *stramineus,* but these do not seem to be more than species characters. The antennae of *stramineus* are 12-segmented; *Nesomyrmex* can have either 11 or 12 segments.

The status of *Nesomyrmex* as a subgenus of *Leptothorax* is maintained for the time being, pending the proper study of both taxa.

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BREVIORA

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PULSED SOUNDS OF THE PORPOISE *LAGENORHYNCHUS AUSTRALIS*

William E. Schevill and William A. Watkins[1]

ABSTRACT. Pulsed sounds of the porpoise *Lagenorhynchus australis* of southern Chile were recorded and analyzed. Most were low-frequency clicks; some had a 2-kHz bandwidth centered near 1 kHz, and others had a 10- or 12-kHz bandwidth with the principal frequency in the lower 5 kHz. These porpoises also produced a rapidly pulsed tonal sound. All these sounds were very low-level and rarely audible at a distance as great as 20 m. We heard none of the whistlelike squeals characteristic of many delphinids.

From 12 November to 11 December 1968 the research ship HERO of the National Science Foundation (Antarctic Research Program) cruised between Valparaiso and Cape Horn, searching for cetaceans and pinnipeds, mostly in the sheltered inland waterways of southern Chile. We were concerned with listening for and recording the underwater sounds of these animals.

The species most frequently seen and collected was *Lagenorhynchus australis* (Peale, 1848), which has been reported from the west coast of Chile south of about S Lat. 40° around Cape Horn to the Falkland Islands. We heard them much less often than we saw them.

Methods. The recordings that are analyzed here were made on 23 November in Canal Messier (at 48° 10′ S) and 1, 3, 5, and 6 December west and south of Navarino Island behind Cape Horn. An Atlantic Research LC-34 hydrophone was used to pick up the sounds. An impedance-matching pre-amplifier (WHOI) was inserted in the cable 30 cm from the hydrophone. Two cable lengths

[1] Contribution No. 2562 from the Woods Hole Oceanographic Institution.

were used, 125 m from R/V HERO and 30 m from HERO's whaleboat. The hydrophone depth varied with local conditions and experiments, from 2 m to nearly 125 m; it was usually suspended 6-8 m from a surface float (a rubber balloon) and allowed to drift as far from ship or boat as cable-length permitted.

Tape recordings were made with either a modified Uher 4400 recorder or a WHOI-built springwound recorder, using a hydrophone amplifier (Watkins, 1963). When the Uher was in use, the system-response was limited to a bandwidth, within 4 db, of 40 to 20,000 Hz; with the WHOI machine, system-response was 20 to 32,000 Hz (within ½ db from 30 to 30,000 Hz). Playback for analysis was on Crown 800 tape recorders. Spectrographic analyses were made on a Kay Electric model 7029A analyzer and amplitude analyses on a Tektronix 535A oscilloscope.

The porpoises were approached as closely and as unobtrusively as possible, but even so, often the only sounds heard from the animals were within the first 5 seconds of the listening attempts. Unfortunately, because of the disturbance of the water by arrival of the boat and the motion of the hydrophone, a longer time than this usually was required before local ambient noise could settle down enough for faint sounds to be recorded. Usually nothing was heard from the porpoises, partly because they were generally taciturn and seemed to produce sounds only occasionally, and partly because their sounds were too faint to be audible except on close approach, within a few meters of the animals. They appeared to be silent when disturbed.

Sounds. The sounds heard from *Lagenorhynchus australis* were all pulsed. Mostly they were clicks produced in short series or slow bursts, but sometimes a rapidly pulsed sound (a buzz) that had a tonal quality was heard. The buzz was the only sound heard from *L. australis* at any distance, and it was produced only occasionally; consequently most attempts to listen to these porpoises were entirely unsuccessful. No squeals (whistles) were heard; this was unexpected since we have heard squeals from other *Lagenorhynchus* (*L. albirostris, acutus, obliquidens,* and the *obscurus* of New Zealand).

These sounds of *L. australis* were low level and generally inaudible beyond about 10-20 m. We estimate that the loudest clicks were no more than −20 db re 1 dyne/cm^2 at 1 m, from known hydrophone sensitivities and tape saturation levels, and

assumed supply voltages and amplifier gains. On only a few occasions were we convinced that we knew which individual produced the sounds that we heard, and therefore our estimates of signal strength and of distance from the hydrophone are but guesses.

The click-sounds were of two types: a broadband click, and a relatively restricted-bandwidth click (narrowband) at predominantly low frequencies. These two clicks never seemed to be mixed. Both types were heard, we thought, from any one individual, with no obvious separation between the different kinds of clicks, and no gradual transition. Though both types of clicks were sometimes heard at slow rates (1 or 2 per sec.), the broadband click was usually produced at a more rapid repetition-rate (20 to 80 per sec.) than the narrowband click (5 to 25 per sec.). The broadband click was shorter and had less energy at low frequencies than the narrowband click. See the table for a comparison of these two clicks.

The broadband click (Figs. 1A and 2) was characterized by a sharp onset, a short duration, as well as a more or less continuous spectrum to 10 or 12 kHz, occasionally to 16 kHz. Analyses of clicks showed a general drop in intensity of 1 to 2 db per 1000 Hz above 5 or 6 kHz. This drop was greater than is consistent with normal frequency-selective absorption for these distances and frequencies, so we assume that this attenuation is characteristic of the click of *L. australis*. The duration of the broadband click was consistently a little less than 1 msec. Because of the general low level of the sounds as well as their usual reduction in intensity at higher frequencies, the clicks were easily masked by background ambient.

The narrowband click (Figs. 1B and 2) was restricted in frequency to the lower 2000 Hz and appeared to have its greatest intensity at or below 1000 Hz. Harmonics did exist, though at greatly reduced levels. Analysis at high gain (but still undistorted) showed some of the narrowband clicks with harmonic frequencies to 5 or 6 kHz. The narrowband click, with a duration of 1.5 to 3 msec., usually occurred at slower repetition-rates (5 to 25 per sec.), and consistently had higher intensity at low frequencies than the broadband click. Perhaps because of its lower-frequency emphasis and therefore better transmission characteristics, the narrowband click was the one most commonly heard.

The third type of sound, the buzz (Fig. 3) was heard on a few

occasions. This buzz had emphasis at discrete higher frequencies, such that both the fundamental and high frequency overtones were predominant in the aural impression of the sound. The buzzes varied in duration from 0.6 to 1.1 sec. They were composed of a pulsed fundamental near 300 Hz (Fig. 4) and strong overtones at 4 to 5 kHz. Two or three sidebands of the pulse repetition-rate (modulation, Fig. 1C) may be noted grouped around the 4- to 5-kHz overtone in spectral analysis (Fig. 3) of these buzzes (see Watkins, 1967). The fundamental frequency of the buzz was more intense than the overtones, yet at greater distances only the 4- to 5-kHz tone (with its associated sideband structure) was audible. This was probably because of higher background ambient at the lower frequencies. The buzz appeared to be produced at a higher level than the clicks.

Discussion. Because of both the pulsed quality of the buzz and its restricted frequency, we suppose that this sound was formed by rapidly repeated narrowband clicks. Singly, the narrowband clicks had few higher frequency components, but in a rapid series the overtones were prominent. This is somewhat similar to sounds produced by *Phocoena phocoena,* composed of a rapid repetition of narrowband clicks to form a continuous sound with selected higher frequency emphases (Schevill, Watkins, and Ray, 1969). We did not find the variation in the overtones of the buzz of *L. australis* that we noted for *Phocoena,* but this may have been due to the limited number of the former's buzz sounds that were recorded well enough for such detailed analysis.

Perhaps the buzz was used in communication and it may have been associated with stress. This could explain its relatively infrequent occurrence. The only time that the buzz was heard when we thought we knew which porpoises were producing it (in Paso Micalvi outside of Seno Grandi, Navarino Island, 6 December), a group of three animals 15 to 20 m distant suddenly seemed to be in a scuffle, darting at and away from each other. This sudden unusual activity coincided with the production of four buzzes, two of them concurrently (Figs. 3 and 4), and so we assume that these sounds were produced by these porpoises.

We have no evidence that *Lagenorhynchus australis* echolocates. If the click sounds were used for echolocation as in some other species (*Tursiops truncatus, Steno bredanensis, Orcinus orca, Phocoena phocoena*), it must have been at relatively close ranges

because of the low level of the clicks. We did not hear any "accelerando" in click series such as is typical of echolocation runs during feeding by these other animals; however, we had no suggestion that the *L. australis* were feeding when the clicks were heard. In fact, the clicks were not consistently associated with apparently investigatory behavior by the animals. Porpoises sometimes passed within a meter of the hydrophone and even appeared to return and examine it without our detecting any sounds. On the other hand, clicks were never heard unless a porpoise was close by.

The two click-types perhaps are equivalent to the two basic click-categories noted for *Tursiops* by Norris, Evans, and Turner (1967). They name these clicks by their function, "discrimination clicks" and "orientation clicks." The discrimination click of *Tursiops* has a reduced bandwidth and emphasis of lower frequencies, while the orientation click has a wide bandwidth. In these respects they match the sounds heard from *L. australis*, though no behavioral correlation was possible.

Although two types of clicks were heard, one with a relatively restricted low frequency and other with broadband characteristics, it suggests the possibility that only one click type exists in reality and the variations noted result from changing orientation by an animal possessing a directional sound system. Other cetaceans have been shown to have such a directional sound field (*Tursiops,* Norris, Prescott, Asa-Dorian, and Perkins, 1961; *Orcinus,* Schevill and Watkins, 1966; *Steno,* Norris and Evans, 1967; and, *Platanista,* Evans in Herald et al., 1969). Our data is insufficient to rule out this possibility completely, but the evidence that we have seems to argue instead for two distinct click types:

1. The click durations of the two types are different. High frequency emphasis in a low frequency click would not shorten the length of the pulse but would simply extend the bandwidth.
2. The two click-types suddenly interchange with no pause between. We have no examples of a gradual shift from one type to the other and we have very few individual clicks whose characteristics are intermediate in form. Some of the subtle variations observed in the higher frequency components of successive clicks of both types, however, may result from such directionality, though we did not have opportunity to observe any correlation of orientation with bandwith.

Because of the difficulties we encountered in hearing the porpoises, we were impressed with the low level of their sounds. We also were acutely aware that it was not high background that obscured their sounds, since the ambient noise levels in this region were actually very low. Without carefully and recently calibrated equipment, such low sound-levels are difficult (and probably meaningless) to assess; however, our limitation much of the time appeared to be the self-noise of the equipment rather than the local ambient background. Perhaps the land barriers shielded the inland channels from the usual open sea sounds and at the same time provided enough shelter so that very little local wind and wave noise was generated. In addition, we recognized very little contribution of sound from other biological sources, and certainly these porpoises had but small influence on the local ambient sound.

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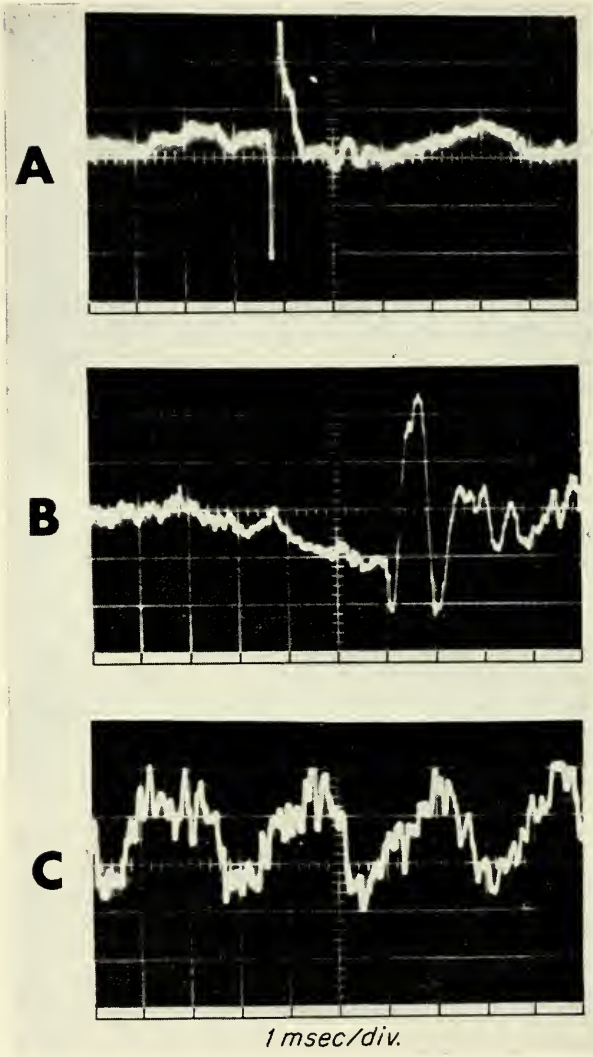

Figure 1. Oscillographic pictures of (A) the broadband click, (B) the narrowband click, and (C) the pulse modulation of the buzz. Ambient noise is superimposed on these sound traces.

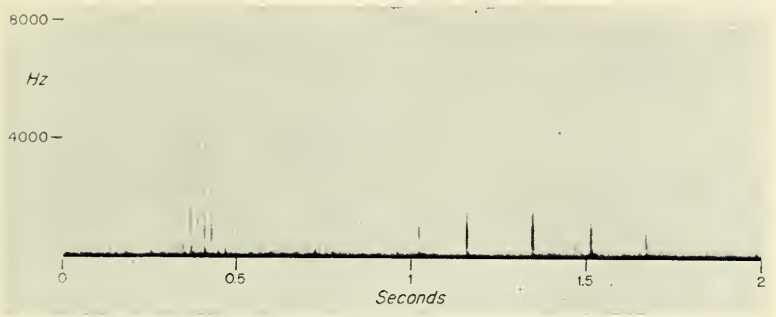

Figure 2. Spectrographic analysis shows a burst of broadband clicks followed by narrowband clicks. Although the latter become much greater in amplitude as the animal comes closer, the frequency spectrum remains relatively restricted. The bandwidth of the analyzing filter is 300 Hz. This figure is the result of a repetitive analysis, with a small horizontal displacement of the paper between analyses to widen artificially the traces of these short-duration sounds for better photographic reproduction.

	Narrowband click	Broadband click
Bandwidth	2 kHz	10 or 12 kHz
Principal frequency	1 kHz or less	from less than 1 to 5 kHz
Duration	1.5 to 3 msec	0.8 to 1 msec
Repetition rate	5 to 25/sec	20 to 80/sec
Intensity (re 1 dyne/cm^2)	−20 db at principal frequency	−20db spread over bandwidth

Table of characteristics of the two types of click heard from *Lagenorhynchus australis*.

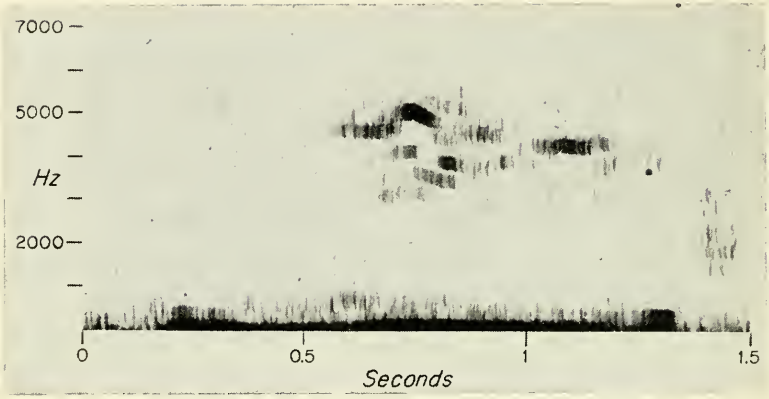

Figure 3. Two simultaneous buzzes have emphasis in the 4- to 5-kHz region as well as a strong fundamental at about 300 Hz. The analyzing filter bandwidth is 300 Hz. Compare Fig. 4.

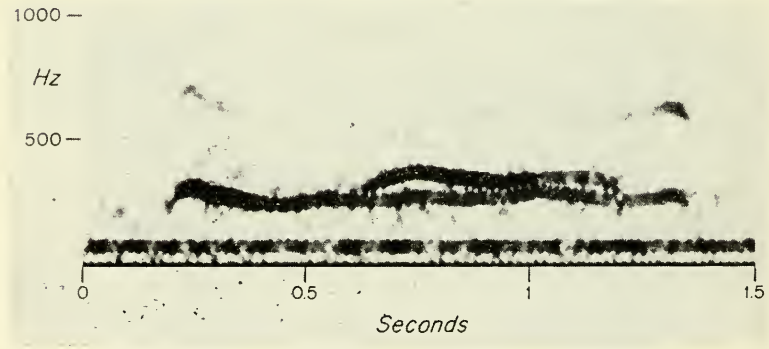

Figure 4. The fundamental frequencies of the same two buzzes shown in Fig. 3 show variation in the region of 300 Hz. The continuous low frequency band is ship's propulsion noise from the HERO about 5 or 6 miles away. The analyzing filter bandwidth is 45 Hz.

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MICROMISCHODUS SUGILLATUS, A NEW HEMIODONTID CHARACIN FISH FROM BRAZIL, AND ITS RELATIONSHIP TO THE CHILODONTIDAE

Tyson R. Roberts

ABSTRACT. A new genus and species of Hemiodontidae, designated as a new subfamily, Micromischodontinae, is described from the lower Rio Negro and Middle Amazon of Brazil. Its osteology is described and figured. It appears to be the hemiodontid genus most closely related to Chilodontidae. The relationship between the functional and replacement teeth of the pharyngeals suggests the probable manner in which the peculiar pharyngeal teeth characteristic of Chilodontidae and Anostomidae evolved. A brief definition is given of the family Chilodontidae.

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Dr. Stanley H. Weitzman, Division of Fishes, U.S. National Museum, suspected hemiodontids and chilodontids might be related and mentioned this to me two or three years ago. He is now working on the relationships of these families and has graciously let me examine unpublished illustrations of chilodontid osteology. I am indebted to Sr. Heraldo Britski, curator of the fish collections of the Museu de Zoologia, Universidade de São Paulo, and leader of the Expedição Permanente da Amazônia when the new fish was collected, for permitting me to prepare its description. Professor George S. Myers, Division of Systematic Biology, Stanford University, Dr. Weitzman and Sr. Britski reviewed the manuscript.

INTRODUCTION

The hemiodontid herein described, collected by the Expedição Permanente da Amazônia[1] in 1967, represents a new subfamily. While lacking certain morphological peculiarities of the highly specialized Chilodontidae, it nevertheless appears to be more closely related to them than is any other hemiodontid. In the light of its discovery, there can be little doubt that Chilodontidae and Hemiodontidae are indeed closely related. Although the pharyngeal teeth of this new form are single cusped, the relationship between functional and replacement teeth on the pharyngeals suggests the primitive condition from which the peculiar multicuspid pharyngeal teeth characteristic of Chilodontidae and Anostomidae presumably evolved. Its highly distinctive trophic structures indicate an unusual mode of feeding, perhaps similar to that of *Bivibranchia,* considered to have the most specialized trophic structures of all characoids. Nevertheless, it represents a line distant from *Bivibranchia* (and the related but less specialized *Argonectes*).

Hemiodontidae are marvelously streamlined, swift-swimming fishes mostly six inches to a foot long. They form small groups in open water in big rivers and lagos. *Hemiodus* are known in Brazil as "voadores" because of their ability to jump. A group of voadores leaping away from predaceous fishes or over a seine net to safety is an impressive sight. Spawning presumably takes place in open water and the young probably grow up in aggregations staying near the bottom in fairly shallow open water. It appears to be unrecorded whether hemiodontids form huge schools or undertake major spawning migrations.

Hemiodontids hitherto known readily fall into two subfamilies, Hemiodontinae and Bivibranchiinae, adults of which have multicuspid teeth in the upper jaw and no teeth in the lower jaw. The minute, unicuspid teeth and other features of the new fish differ so greatly from previously known forms that it represents a new subfamily.

[1] The Expedição Permanente da Amazônia, under the direction of Dr. P. E. Vanzolini, is a cooperative effort among the Museu de Zoologia, Universidade de São Paulo (MZUSP); Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus; and Museu Goeldi in Belem. It is financed by the Fundação de Amparo à Pesquisa of the state of São Paulo. Much attention has been devoted to fishes since fieldwork began in 1967. The fish collections are housed at MZUSP.

MICROMISCHODONTINAE, new subfamily

Highly streamlined, fusiform fishes typically hemiodontid in habitus and osteology. Teeth pedicellate, with a single strongly recurved cusp; tooth crowns black or brownish black, stalks deep yellow or yellowish brown. Each dentary and lower pharyngeal with two, nearly coextensive rows of 50–60 teeth. Teeth on upper pharyngeal arranged in numerous, extremly regular rows (as in Anostomidae). Upper jaw with a broad frenum, nonprotractile; roof of mouth with fine, linear ridges, without valvelike structures. Gill rakers elongate and numerous, with six to eight papillae on either side of each gill raker, forming a dense carpetlike lining to gill chambers. Lower pharyngeals exceptionally long and slender, tooth-bearing for virtually their entire length. Upper limb of second gill arch with a fleshy membrane forming a sort of pocket anterior to upper pharyngeals. Posterior face of fourth gill arch with ordinary gill filaments; face of fifth gill arch smooth; no dorsal diverticulum between fourth and fifth arches. Stomach reversed, that is, with cardiac portion (entrance of esophagus) posterior and pyloric portion anterior in position; pyloric caeca about thirty, not well differentiated; length of intestine in preserved specimens about equal to standard length, forming a single loop upon leaving stomach, then passing straight to vent. Posterior chamber of swim bladder about one-half of standard length or six times length of anterior chamber, terminating in a fine taper which extends to above base of last anal fin ray. Adipose eye-lid thick and very strong, extending from immediately behind nostrils well onto gill cover, and with a narrow vertical slit over the pupil (Fig. 1).

Cranial fontanels as in chilodontids and other hemiodontids, anterior fontanel linear and narrow, posterior fontanel slightly wider (Fig. 2). Size, shape, and position of jaw bones as in *Hemiodus;* a peculiar fenestra in tooth-bearing portion of dentary (a similarly located fenestra present in *Hemiodus,* absent in foreshortened dentary of chilodontids). Anterior end of ethmoid with small lateral knobs. Circumorbital series with simple antorbital, supraorbital, and full complement of six infraorbitals; first infraorbital smaller than those succeeding it (enlarged in Chilodontidae), second through fourth infraorbitals each slightly larger than the preceding one. Branchiostegal rays five (five in *Hemiodus* and *Argonectes,* four in *Chilodus* and *Caenotropus*); proximal end

of fourth branchiostegal ray greatly expanded; hyoid bar generalized (apparently highly specialized in Chilodontidae). Gill membranes free from isthmus, united to each other at a point below middle of eye (broadly united to isthmus in chilodontids); isthmus scaled anterior to cleithral symphysis (scaleless in chilodontids). Three postcleithra; third (lowermost) postcleithrum with a lamellar, posteriorly directed extension (as in *Hemiodus*). Weberian apparatus and caudal skeleton without unusual modifications. Forty vertebrae, including Weberian apparatus.

MICROMISCHODUS, new genus

Nomenclatural type-species: M. sugillatus, new species

Body fusiform and highly streamlined. Secondary sexual dimorphism unknown (specimens at hand collected in November and December, with unripe gonads). Cranial roof smooth. Sides of head largely covered by adipose eye-lids. Nares nontubular, close-set and separated only by a flap flush with surface of head. Tip of snout extends slightly beyond included lower jaw. With mouth fully opened, gape almost vertical and about as large as eye diameter. With mouth closed, dorsoposterior edge of maxillary slips under first infraorbital bone; maxillary not extending as far back as anterior margin of eye, but only to below posterior nostril. Toothless portion of lower jaw (posterior to rictal membrane) about four or five times longer than tooth-bearing portion. Articulation of lower jaw below middle of eye; rictal membrane below nostril, distinctly in front of anterior orbital rim. Lateral line complete, slightly decurved anteriorly, then running just below lateral midline of body to last scale row on caudal base.

Origin of dorsal fin midway between snout tip and base of caudal fin. Anal fin small. Caudal fin deeply forked. Dorsal, anal, and median caudal fin rays with well-developed, overlapping, membranous lappets or alae (Fig. 1). Similar structures occur in many fast-swimming lower teleosts, including various other characoids, some cyprinoids and clupeoids, and *Chanos*.

Known by a single species from the Middle Amazon and lower Rio Negro in Brazil.

Derivation of name. Micromischodus is from the Greek *micro,* small, little; *mischos,* stalk, petiole, peduncle; and *odous (odon), odontos,* masc., tooth.

M. SUGILLATUS, new species
Figure 1

Note. Standard lengths are used throughout this paper. Unless stated otherwise, proportional measurements are expressed as times in standard length. Counts and measurements are given for the holotype first, followed in parentheses by the ranges for the paratypes.

Holotype. MZUSP 6773, 152.0 mm, Igarapé Tarumãzinho, 15 km NW of Manaus, on the left bank of the Rio Negro, Estado do Amazonas, 17–18 November 1967.

Paratypes. MZUSP 8870, six specimens 125.0–144.6 mm, same data as holotype; MZUSP 6691, four specimens 107.3–137.1 mm, Rio Negro, arredores de Manaus, Estado do Amazonas, 15–23 November 1967; MCZ 46718, two specimens 118.4 and 137.1 mm, Rio Canumã, Canumã (near Maués), Estado do Amazonas, 28–29 November 1967; MCZ 46719, seven specimens 79.5–108.9 mm, Igarapé do Rio Jamari, Terra Santa, Estado do Pará, 14 December 1967.

Proportional measurements. Greatest body depth (at origin of dorsal fin) 4.1 (4.0–4.5). Greatest body width (below dorsal fin) 5.7 (5.6–6.6). Least depth of caudal peduncle 11.4 (11.3–12.4). Distance from snout-tip to dorsal origin 2.01 (1.94–2.08). Length of caudal peduncle 7.45 (6.4–7.8). Head 3.4 (3.1–3.4). Eye 3.9 (3.4–4.1) in head. Bony interorbital space 3.8 (3.5–4.1) in head. Snout 3.5 (3.4–3.8) in head. Width of mouth (measured to outer sides of maxillaries) 4.1 (4.1–4.7).

Fins. Fins, excepting caudal, scaleless. Dorsal fin rays 11 (11 in all paratypes except one with 10), first two rays simple, last ray divided to its base. Proximal two-thirds to three-quarters of each ray with well-developed membranous lappets or alae, largely overlapping when fin is depressed. Dorsal fin margin falcate. Height of dorsal fin 4.7 (4.3–4.8). Base of dorsal fin 9.2 (8.1–10.3). Anal fin small, about one-third as large as dorsal fin, with similar membranous lappets. Anal rays 10 (10), first two rays simple, last ray divided to its base. Height of anal fin 8.2 (7.4–8.3). Anal fin margin falcate. Base of anal fin 12.4 (11.8–13.4). Caudal fin deeply forked. Lower caudal lobe slightly larger than upper caudal lobe, with its upper margin slightly convex (Fig. 1). The lower caudal lobe is similarly modified in other

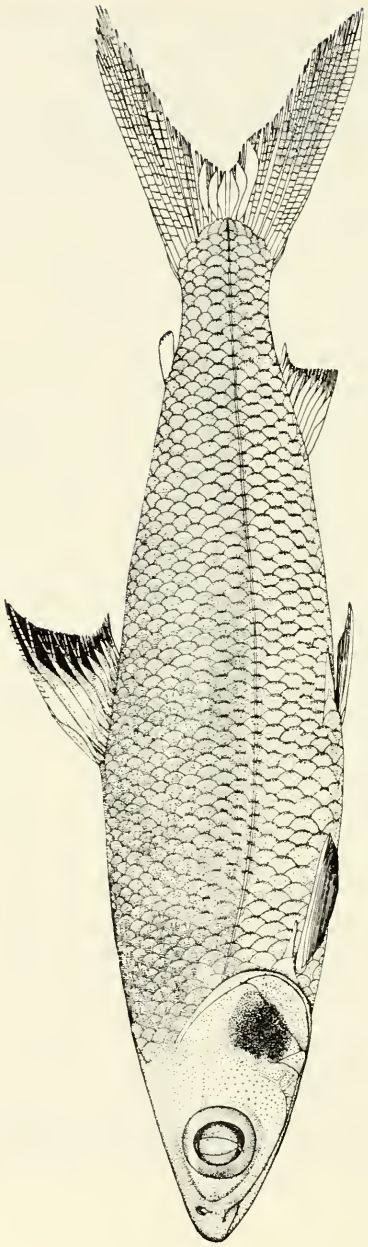

Figure 1. *Micromischodus sugillatus*, holotype. MZUSP 6773, 152.0 mm in standard length.

fast-swimming characoids, for example in *Hydrocynus goliath* (Boulenger, 1899, pl. 11). Principal caudal rays 10 + 9. Median four to six rays with well-developed lappets. Procurrent rays moderately numerous (9 + 7 in 125-mm specimen), unspecialized. Adipose fin small, its base over posterior portion of anal fin base. Pectoral and pelvic fins with two or three peculiarly thickened and elongated scales forming a sheath for edge of outermost rays. Pectoral fin rays 21 (18–22). Length of pectoral fin 6.3 (5.3–6.5). Pelvic fin rays 11 (11), outermost ray only unbranched. Length of pelvic fin 7.0 (6.1–7.2).

Scales. Scales cycloid, or with laciniate (but not ctenoid) borders. Body completely scaled, 57 (56–64) scales in a lateral series; about 21 (16–22) predorsal scales (irregularly aligned); 11 (11 or 12) scales between lateral line and dorsal origin; 4 (4) scales between lateral line and pelvic insertion; 20 (17–22) scales between last dorsal ray and adipose fin; 15 (14–16) scales along midline between symphysis of cleithra and pelvic base; and 16 (16–18) scales around caudal peduncle. Prepelvic scales below lateral line gradually increasing in size ventralwards; scales on abdomen about two or three times larger in diameter than scales above lateral line. Caudal fin beyond hypural fan with two or three rows of scales.

Coloration in alcohol. After two years in preservative (fixed in formalin while alive and transferred to ethyl alcohol within a few months) the specimens are straw colored, darkest above. The most notable feature is the solid black or blue-black color on the membranes between the distal halves of all of the dorsal fin rays (but not on the rays themselves). (The hemiodontid *Argonectes scapularis* and chilodontid *Tylobronchus maculosus* have similarly marked dorsal fins.) Pectoral, pelvic, anal, and adipose fins colorless; caudal fin dusky, lower lobe of caudal becoming darker (but not as dark as dorsal fin) near its tip. A faint longitudinal stripe running length of the body but stopping at shoulder, not running through eyes or onto caudal fin. Above lateral line fine melanophores lie beneath the scales and in concentrations paralleling exposed scale margins. Below lateral line melanophores almost entirely absent in some specimens; in other specimens melanophores are virtually absent beneath the scales but are present along the scale margins. The reticulated pattern of vertically oriented spots thus produced is similar to the pattern present in

all Chilodontidae, except that since the scales are much smaller, the spots are small and not as dark. In all specimens body distinctly lighter below lateral line than above. Gill cover marked by an indistinct dark oval patch caused by a concentration of melanophores in the membrane lining inside of gill cover, which shows through the opercular bones.

The trivial name *sugillatus* (Latin: *sugillo, -atus,* beaten black and blue; *sugillatum,* black and blue spot, bruise) refers to the coloration on the dorsal fin and opercles.

Ecological notes. According to Sr. Britski, specimens of *M. sugillatus* were collected by seining along shore in lakes or places with slow-flowing, black or crystalline water. A very large number of species, predominantly characins, was obtained at these localities. The stomach contents of specimens from the Igarapé do Rio Jamari include an assortment of bottom material, including many of what appear to be droppings of small fishes. Very small insects are well represented, including larval Diptera and, most abundant, a corixid (identified by Dr. John Lawrence) about 1.5 mm long. These are about the largest organisms in the stomach contents.

OSTEOLOGY
Figures 2–15

Illustrations of the osteology of *M. sugillatus* are based on a 125.0-mm paratype from MZUSP 8870. Supplemental observations were made on a 102.2-mm paratype from MCZ 46719. The nomenclature of bones follows Weitzman (1962) except that "vomer" and "intercalar" are used in place of "prevomer" and "opisthotic."

Cranium (Figs. 2–4). Roofing bones of skull smooth and flattened. Cranial fontanels narrow, complete. Anterior fontanel linear and about half as wide as posterior fontanel for almost its entire length, but widening immediately in front of epiphyseal bar. Ethmoid narrow, with two lateral knobs anteriorly articulating with either premaxillary, ventro-lateral laminar projections immediately posterior to these knobs, and a median cleft in its posterior half (Fig. 2). Supraoccipital crest flat, not extending as far as end of cranium. Posttemporal fossae well developed. Dilator groove well developed, frontal participating in its formation; dorsal limit of

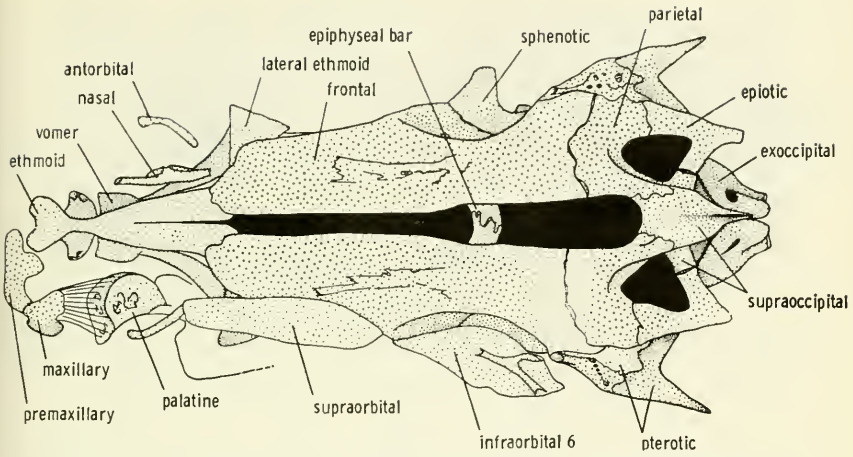

Figure 2. Cranium of *Micromischodus sugillatus* (dorsal view). All osteological figures based on 125-mm specimen from MZUSP 8870.

dilator groove marked by a concavity in dorsolateral margin of frontal bone; sphenotic spine lamellar, rounded at tip.

Ethmoid separated from vomer by a cartilaginous septum (indicated by heavy stippling in Figure 3). Vomer with peculiar anterior knoblike processes on either side. Lateral ethmoid relatively large, with elongate, strutlike process articulating with knoblike process of vomer (Figs. 3 and 4) and a small median projection firmly articulated to antero-ventral corner of rhinosphenoid. Rhinosphenoid large, sharing strongly interdigitating sutures with antero-ventral projection of orbitosphenoid (Fig. 3). Cartilaginous septum between dorsal edge of rhinosphenoid and roof of cranium and another between ventral margin of rhinosphenoid and parasphenoid (cartilage indicated by heavy stippling in Figure 3). Rhinosphenoid and orbitosphenoid not directly contacting parasphenoid. Parasphenoid deeply cleft posteriorly, the thin divisions thus formed cleft at their tips (Fig. 4; compare with Weitzman, 1962, fig. 4 of *Brycon* on p. 60; and Roberts, 1969, fig. 20 of *Acestrorhynchus* on p. 463). Intercalar well developed. Pterotic with strong posteriorly directed spine.

Jaws and jaw suspension (Figs. 2, 5–7). The size and shape of the jaw bones and their relationships to each other are similar

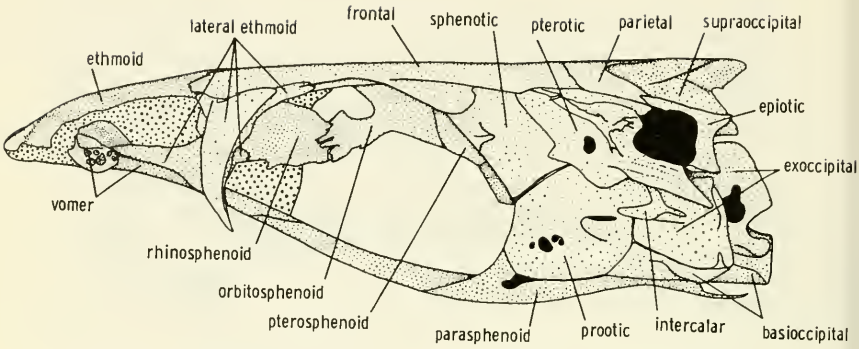

Figure 3. Cranium of *Micromischodus sugillatus* (lateral view).

to those in *Hemiodus*. Premaxillary with a slender, medially directed symphyseal process, round in cross section and blunt at the tip, which approximates but does not articulate or contact its opposite fellow. Lateral surface of premaxillary with a shelflike projection posterior to which is a groovelike depression into which snugly fits anterodorsal corner of maxillary. Dorsal portion of

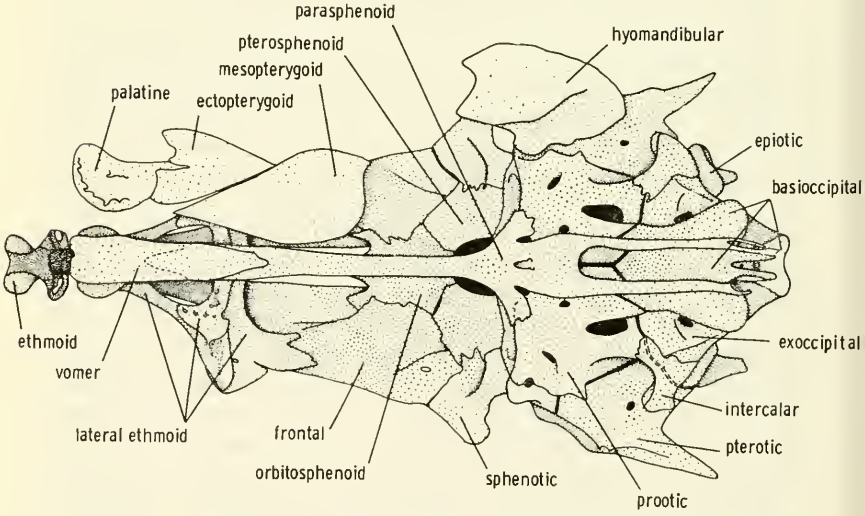

Figure 4. Cranium of *Micromischodus sugillatus* (ventral view).

premaxillary and maxillary firmly embedded in a tough connective tissue that binds them to tip of ethmoid although they do not contact it. Maxillary with dorsoposterior corner expanded and connected by a broad, strong ligament to palatine (Fig. 2). Maxillary bearing a short segment of cephalic sensory canal (Fig. 5).

Dentary with a slender, median symphyseal process, round in cross section, blunt at the tip which approximates and is strongly joined by ligaments to its opposite fellow. Tooth-bearing portion of dentary elevated; rictal membrane attaches maxillary to lateral surface of elevated portion of dentary. Portion of dentary posterior to gape gradually diminishing in width, about twice as long as portion anterior to rictus; articulation with quadrate beneath

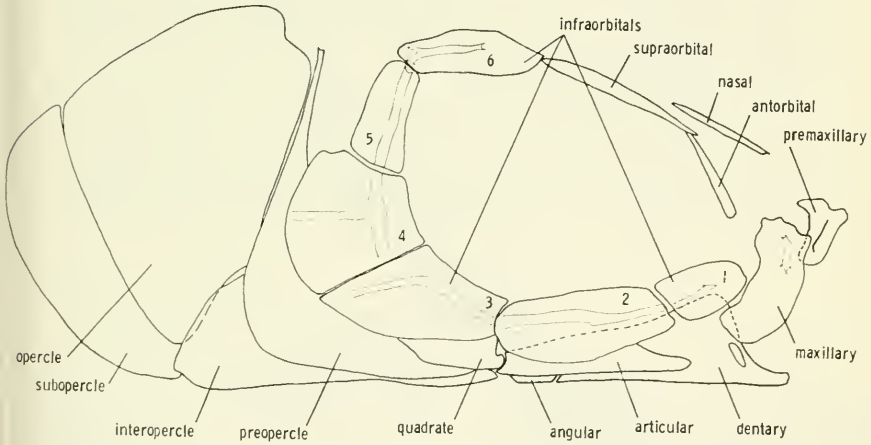

Figure 5. Jaws and facial bones of *Micromischodus sugillatus* (lateral view).

middle of eye. Elevated portion of dentary with a peculiar fenestra below part of the tooth rows (Figs. 5–7); a fenestra identical in shape and position occurs in the toothless dentary of *Hemiodus* but is lacking in chilodontids.

Premaxillary with about 14 minute moveable teeth. Maxillary toothless. Dentary with two coextensive rows of minute moveable teeth. The 125-mm specimen has about 54 teeth in outer row and about 60 (slightly smaller) teeth in inner row, uppermost ten

of which are nonpedicellate; replacement teeth much in evidence (Fig. 7).

The palatine arch presents no unusual features. Metapterygoid-quadrate foramen well developed. Hyomandibular well separated from mesopterygoid.

Facial bones (Figs. 5–6). Facial bones present no unusual features. Circumorbital series complete. Nasal bone tubular, laminar projections minute. Antorbital slender, strutlike. Infraorbitals six; infraorbitals 2–4 gradually increasing in size over ones preceding them. Infraortibal 1 not enlarged. Infraorbitals 3 and 4 with tubes from postorbital branch of cephalic sensory canal system leading to their posterior margin (Fig. 5).

Posterior bony margin of gill cover formed largely by subopercle; subopercle with well-developed, dorsally-projecting spine at anteroventral end. Preopercle with a slender tubular extension dorsally. Suprapreopercle absent.

Visceral arches (Figs. 8–10). Hyoid arch without unusual features. Branchiostegal rays five (as in *Hemiodus, Argonectes*), first four articulating with ceratohyal, fifth with epihyal. Proximal end of fourth where it connects with ceratohyal greatly expanded (see Fig. 9).

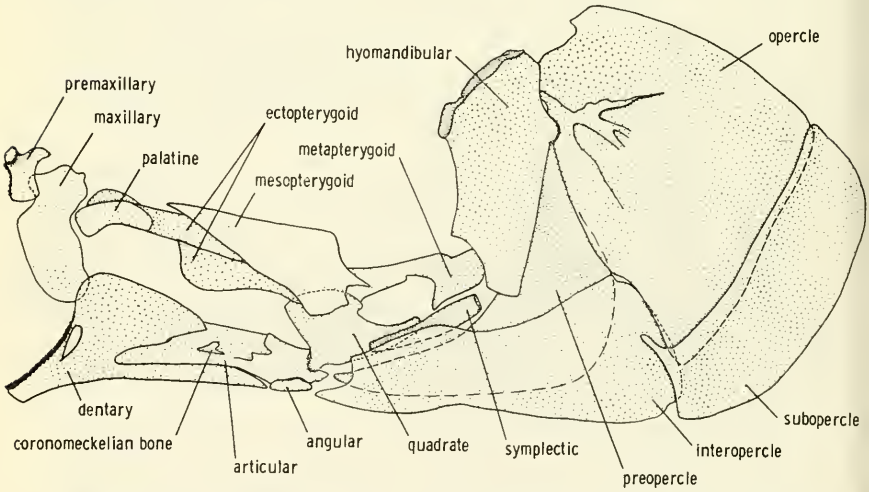

Figure 6. Jaws, jaw suspension, and opercular bones of *Micromischodus sugillatus* (internal view).

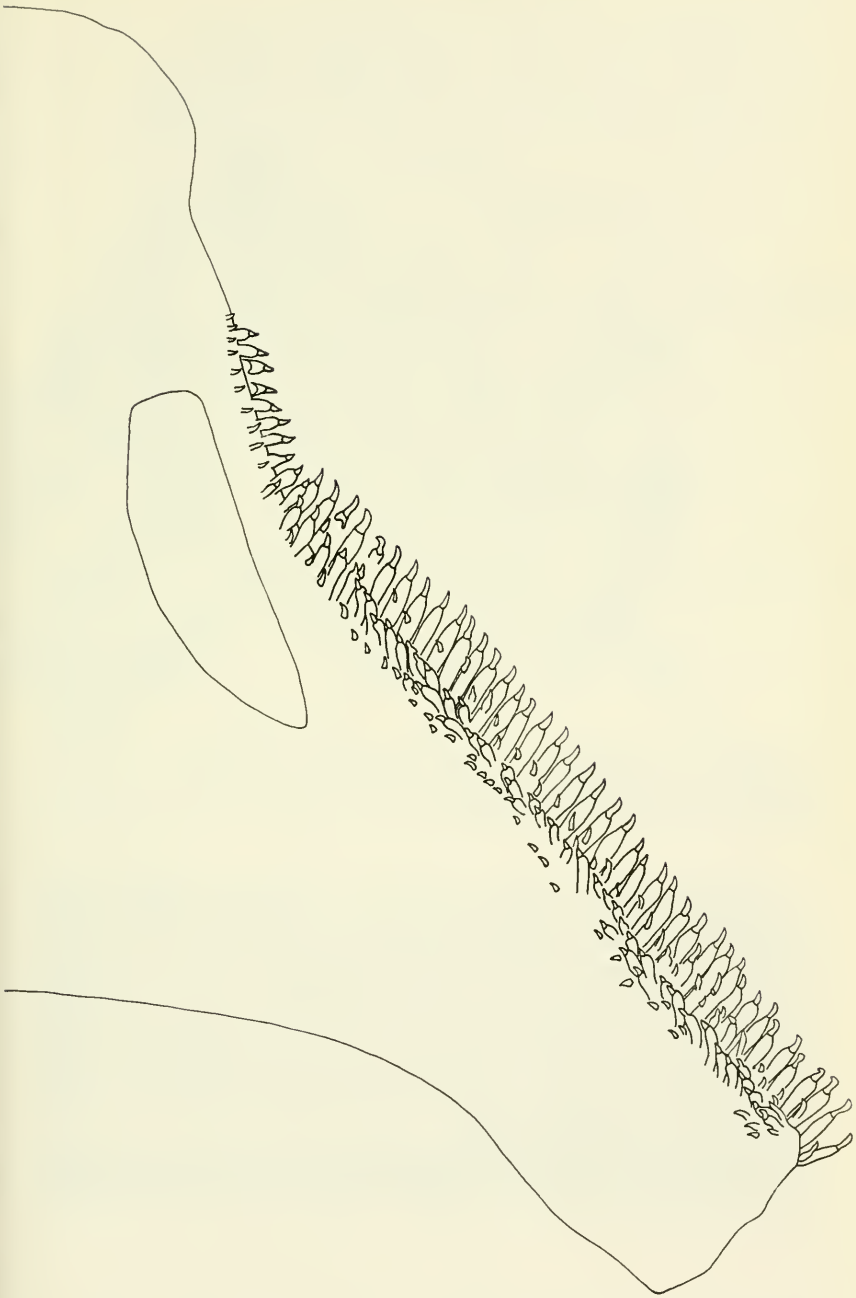

Figure 7. Tooth-bearing portion of dentary of *Micromischodus sugillatus* (internal view).

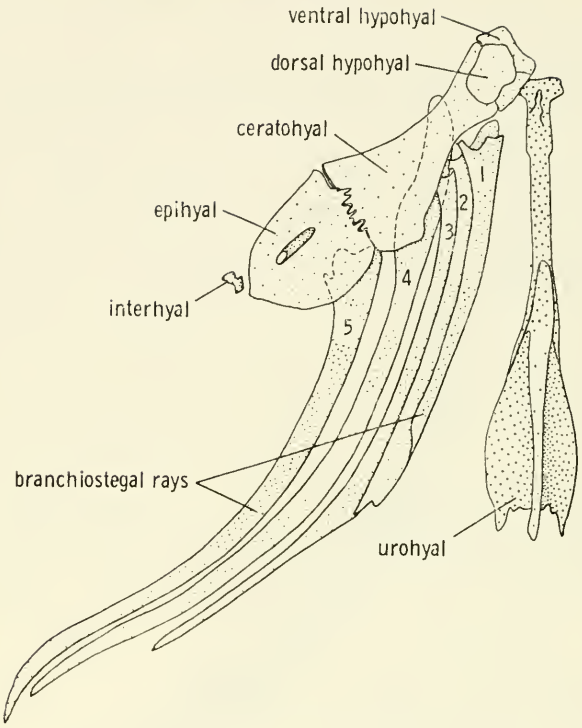

Figure 8. Hyoid arch, branchiostegal rays, and urohyal of *Micromischodus sugillatus* (dorsal view).

Pharyngeal teeth (Figs. 9 and 10). Lower pharyngeals peculiarly elongate and bearing two rows of teeth for virtually their entire length. The recurved crowns of the teeth in anterior row on lower pharyngeal project forward; replacement teeth lie anteriorly to their bases (Fig. 10A). On the trailing edge of the lower pharyngeals is a row of smaller teeth with the recurved crowns projecting backwards; replacement teeth lie posterior to their bases (Fig. 10B). In 125-mm specimen about 64 teeth in anterior row and 60 in posterior row.

At first glance the anterior and posterior rows of lower pharyngeal teeth each appear to constitute two rows. This is because

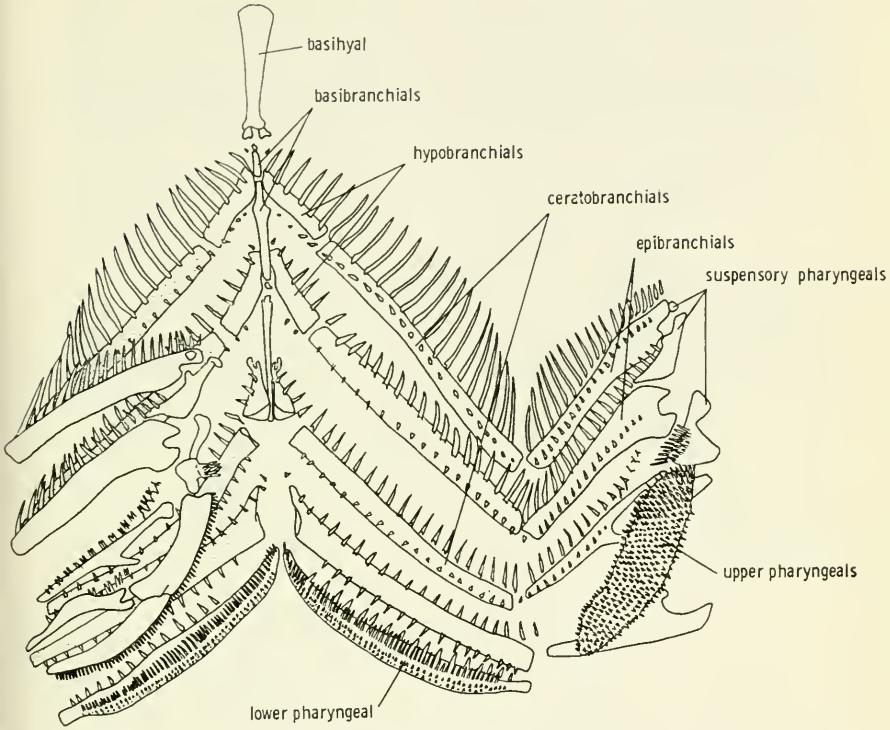

Figure 9. Gill arches of *Micromischodus sugillatus* (dorsal view). Left side in normal position, right side with uppermost elements pinned out and to the side.

not all of the teeth have assumed the "definitive" functional position; teeth just coming into position are out of line with the rest. Since none of the teeth are ankylosed to the bone, the borderline between teeth in functional position and replacement teeth is indistinct. Evidently some of the replacement teeth are "functional" before they are in the definitive functional position, and even before the functional teeth they are about to replace have fallen out. Tooth replacement is much in evidence, and probably occurs in waves proceeding the length of the lower pharyngeals. In some places a functional tooth may have two replacement teeth at its base (see Fig. 10B). These observed characteristics are

highly suggestive of the sort of situation from which the pedicellate multicuspid pharyngeal teeth of Chilodontidae and Anostomidae presumably evolved. If this view is correct, then successive cusps fused below the main cusp to the stalklike base are phylogenetically equivalent to successive generations of replacement teeth.

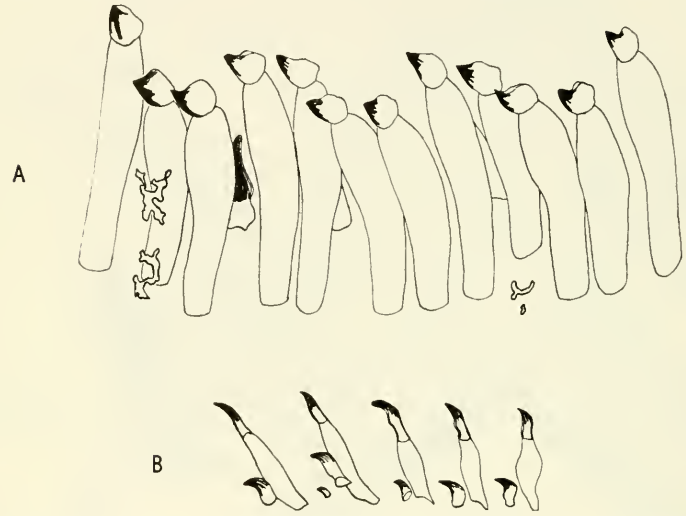

Figure 10. Lower pharyngeal teeth of *Micromischodus sugillatus* (posterior view). A, anterior row; B, posterior row.

The upper pharyngeals bear numerous regularly arranged rows of teeth in which the crowns project backwards (in opposition to crowns of teeth in anterior row of lower pharyngeal which point forwards). The third suspensory pharyngeal bears a small patch of similar teeth. Gill rakers edentulous.

The pharyngeal teeth, although morphologically similar to those in the jaws, are more solidly implanted and much larger (except for the teeth in the posterior row on lower pharyngeal); still, they are considerably smaller than the greatly enlarged and very solidly implanted pharyngeal teeth of Chilodontidae and Anostomidae. In the 125-mm specimen the teeth in the upper jaw are about 0.2 mm long; the teeth in the outer row of the lower jaw are 0.4 mm long; the teeth on the upper pharyngeal and in the anterior row on

the lower pharyngeal are 1.0 mm long; and the teeth in the posterior row on the lower pharyngeal are 0.4 mm long. The highly regular arrangement of tooth rows on the upper pharyngeal is suggestive of the regular rows on the upper pharyngeals of Anostomidae. The arrangement of teeth in the lower pharyngeals is unique. In most characoids, including *Hemiodus,* the teeth are in several irregular rows on an expanded portion of the lower pharyngeal near the midline; the distal half of the lower pharyngeal is usually toothless.

Weberian apparatus (Figs. 11 and 12). Weberian apparatus showing no unusual features, similar to that of typical Characidae. Neural arch pedicle of third vertebra with a dorsally directed process tightly bound into a groovelike fossa in base of neural arch complex. Base of neural arch complex extends posteriorly so that its posteroventral surface almost contacts entire anterior face of neural spine of fourth vertebra. Rib of fifth vertebra with a medially directed process ligamentously attached to os suspensorium. Transverse process of third vertebra, which cradles intercalarium, well developed. Lateral process of os suspensorium very

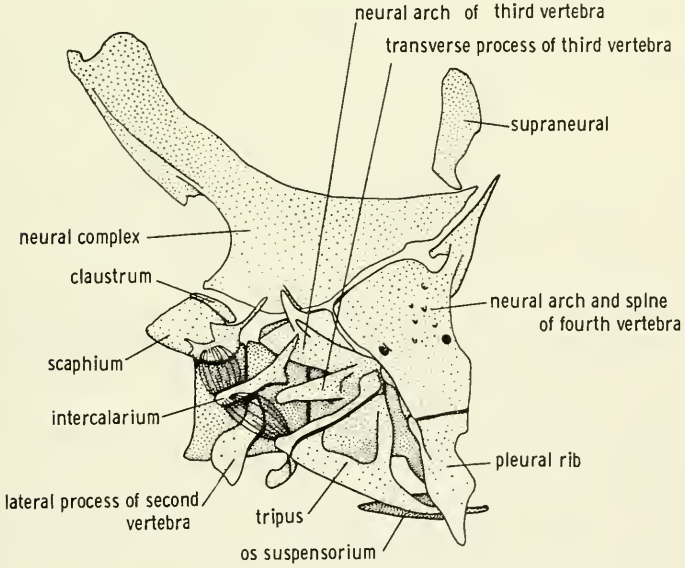

Figure 11. Weberian apparatus of *Micromischodus sugillatus* (lateral view).

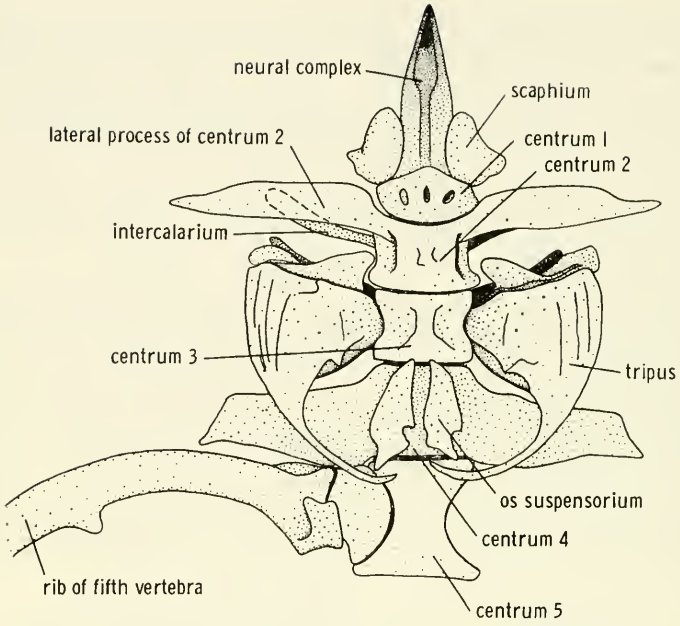

Figure 12. Weberian apparatus of *Micromischodus sugillatus* (ventral view).

large, overlying transformator process of tripus. Neural arch of third vertebra extending far anteriorly over second centrum (Fig. 11). Lateral process of centrum 2 very large.

Pectoral girdle (Fig. 13). Pectoral girdle without unusual specializations. Three postcleithra. Most distinctive feature is lamellar projection from proximal part of third postcleithra (similar process present in *Hemiodus*); in other characoids third postcleithrum slender for entire length.

Pelvic girdle (Fig. 14). Ischiac process well developed; four radials; pelvic splint present; rays invariably 11.

Caudal skeleton (Fig. 15). Caudal skeleton generalized. Hypurals 5 and 6 fused, rest separate. Two uroneurals. Three epurals. Principal caudal rays invariably 10 + 9. Nine upper and seven lower procurrent rays in 125-mm specimen.

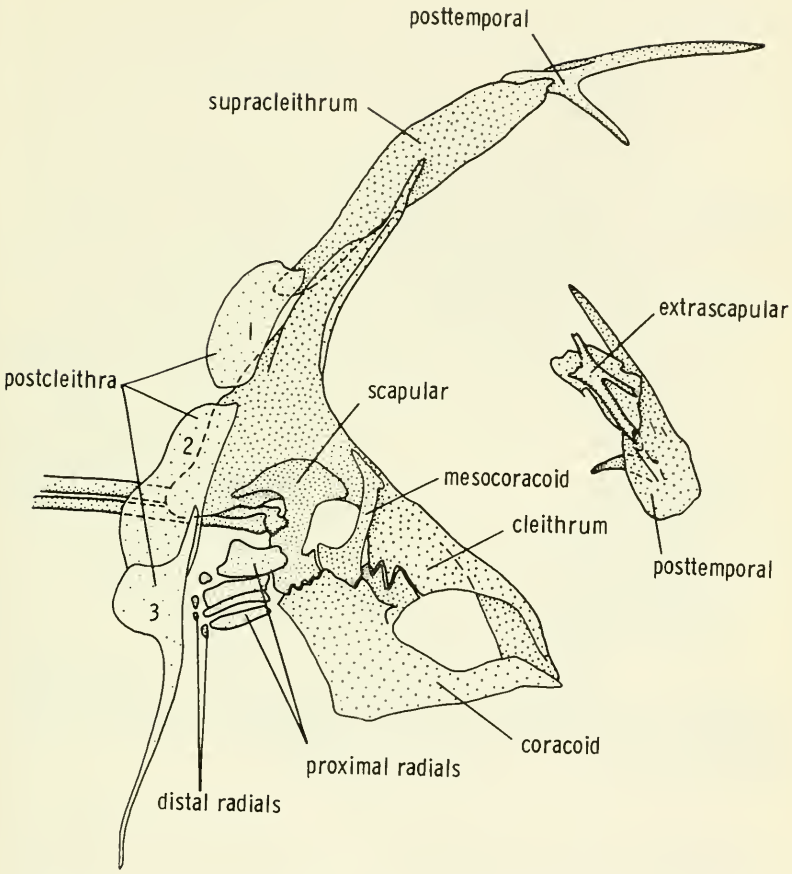

Figure 13. Pectoral girdle of *Micromischodus sugillatus* (internal view). Inset: external view of extrascapular and posttemporal.

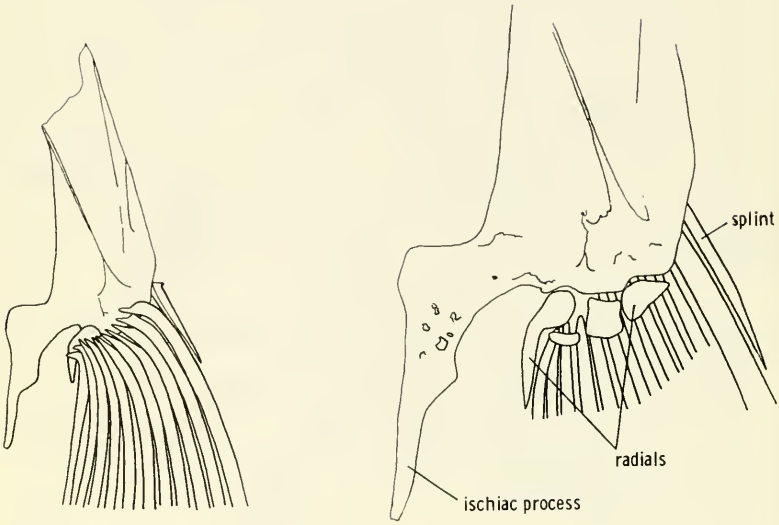

Figure 14. Pelvic girdle of *Micromischodus sugillatus* (ventral view). Enlarged view on right side with radials exposed by removal of outer half of each lepidotrich.

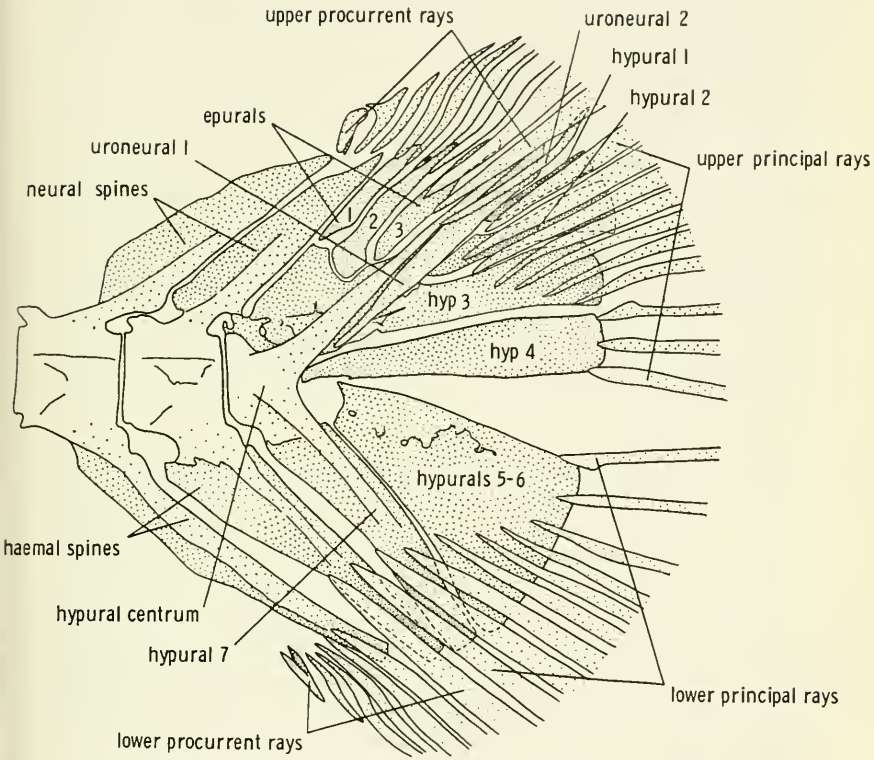

Figure 15. Caudal skeleton of *Micromischodus sugillatus* (lateral view).

DEFINITION OF THE FAMILY CHILODONTIDAE

A definition of the family Chilodontidae is given here primarly for comparison with Micromischodontinae. This definition is not the result of thorough researches of all taxa involved; it is anticipated that studies in progress by Weitzman will greatly extend knowledge of the group. Trophic structures were emphasized in defining Micromischodontinae, as they will also be in the following definition. Modification of trophic structures has been the main theme in the great adaptive radiation of characoids. Trenchant differences in feeding habits and trophic structures characterize most genera and higher taxa, and it is natural to emphasize these differences in definitions. Some important modifications which do not directly involve trophic structures are nevertheless strongly linked to modes of feeding, viz., swimming position in Chilodontidae and Anostomidae. Parenthetically, any attempt to work out a phyletic classification of the higher characoid taxa must necessarily give major consideration to the evolution of their trophic structures.

Chilodontidae. Characoid fishes reaching about 150 mm in standard length which spend much of the time in an oblique head-down swimming position. In many regards—including position of fins, approximate number of fin rays, and general cranial osteology—they are like Hemiodontidae. They differ from the Hemiodontidae in having the skull, including the lower jaw, and the whole body relatively short, and in their trophic modifications. Number of scales considerably less than in Hemiodontidae (about 25–30 vs. 50–125). Pectoral fin with 13–16 rays (18–23 in Hemiodontidae). Vertebrae including Weberian apparatus 33 in *Chilodus,* 35 in *Tylobronchus* (Eigenmann, 1912: 271–273).

Lower jaw behind rictal membrane greatly foreshortened; first infraorbital enlarged; jaw teeth and pharyngeal teeth reduced in number. Premaxillary with a single row of conical (*Caenotropus, Chilodus*) or bicuspid (*Tylobronchus*), stalked teeth; lower jaw with a single row of conical, stalked teeth (*Chilodus, Tylobronchus*) or no teeth in large adults (*Caenotropus*). Teeth embedded in lips and freely moveable, not ankylosed to jaw bone. Upper and lower pharyngeals with enlarged teeth with two, three, or more cusps ossified to a stout, stalklike base. In *Chilodus,* lower pharyngeal teeth confined to a small, round patch in the

center of a large, bowllike depression formed by concave dorsal surfaces of the greatly expanded (and highly peculiar) lower pharyngeal bones. Posterior face of fourth arch and exposed face of fifth arch bearing complementary rosettes of what appear to be modified gill filaments covered with tiny papillae and with tough hooklets at their distal ends, evidently adapted to food selection (see Géry, 1964, fig. 2 on p. 63). Gill rakers reduced in number; bony lamellae of gill rakers reduced or absent in *Chilodus* (invariably well developed in Hemiodontidae). Gill membranes tightly bound to posteriormost part of isthmus, i.e., immediately in front of base of pectoral girdle (free in Hemiodontidae). Hyoid bar highly modified. Branchiostegal rays four (verified in *Caenotropus* and *Chilodus*). Isthmus scaleless. Caudal fin less forked and anal fin larger than in Hemiodontidae. Membranous lappets on dorsal, anal, and caudal fins reduced. Adipose eyelid reduced. Distal half of dorsal fin wholly or partly covered with a black or bluish black color, which partly breaks up into spots in *Chilodus;* sides of body with a punctuate color pattern, spots borne on individual scales, and usually with a dark, longitudinal stripe on the midline extending through the eye onto the middle of the caudal fin.

I have pointed out (Roberts, 1969: 424, 442) that Chilodontidae and Anostomidae have similar multicuspid pharyngeal teeth, and suggested that perhaps the Chilodontidae should be regarded as a subfamily of Anostomidae. In the light of the present study, I still feel that the two groups are closely related, but am inclined to regard Chilodontidae as of family rank. The chilodontids are set off from Anostomidae by the specialized structure of their fourth and fifth gill arches and form a small group of clearly related forms. And while it seems clear that the chilodontids are related to the Anostomidae, the anostomid genus closest to them cannot be singled out. Furthermore, the chilodontids show equally clearly indications of relationship with Hemiodontidae—a relationship closer than I previously had thought likely. Thus the reasonable solution for now, and one which may prove of lasting value, is recognition of three families, Hemiodontidae, Chilodontidae, and Anostomidae. It will be noted that the Anostomidae form a "well-knit" group of some ten or eleven genera.

COMMENTS ON HEMIODONTINAE AND BIVIBRANCHIINAE

The Hemiodontinae comprises *Hemiodus* (but see Géry, 1963), with numerous species differing sharply in color patterns and scale counts (see Böhkle, 1955) and two or three closely related genera of doubtful distinctness and confusing nomenclatural status (see Géry, 1961; 1963). The Bivibranchiinae comprises three quite distinct genera, each with but one or two species, *Argonectes* (Böhlke and Myers, 1956), *Atomaster* (Eigenmann and Myers, 1927) and *Bivibranchia.* Briefly, the Bivibranchiinae have a highly protractile upper jaw with tricuspid teeth, and highly specialized trophic structures in the roof of the mouth and in the pharynx. The nature of their pharyngeal teeth has yet to be elucidated. Of the three genera, *Argonectes* is least specialized and approaches in some respects the Hemiodontinae, which have relatively nonprotractile upper jaws with multicuspid teeth of eight or nine cusps, and relatively generalized oral and pharyngeal passages.

In neither of the two subfamilies do adults have teeth in the lower jaw. The dentition of young *Hemiodus,* however, is very different from that of adults. According to Géry (1963: 604), in alevins of *Hemiodus* (tentatively identified as *H. unimaculatus*) up to 17.3 mm in standard length, there are but six to eight teeth on the premaxillaries, these teeth having fewer cusps than those in adults, and the dentary bears four or six very small conical teeth, visible only with strong magnification. We may feel fairly secure in supposing (Roberts, 1967) that the earliest dentition in *Hemiodus* consists of small conical teeth in both upper and lower jaws. As *Hemiodus* grow, presumably the upper jaw teeth increase in number and are replaced by teeth with successively more cusps, whereas the conical teeth in the lower jaw are replaced relatively few times, if at all, and drop out altogether at a fairly early stage.

Menezes and Oliveira e Silva (1949) reported that stomach contents of *Hemiodus parnaguae* from the Rio Parnaíba in Piauí, Brazil, contain mud, algae, and remains of higher plants. No information is available on food habits of Bivibranchiinae. I suspect that *Bivibranchia* take a mouthful of sand, sort food particles out in the gill chambers and then spit the sand out of the mouth. Géry (1969: 836) stated that *Bivibranchia* bury themselves in sand "like sand-eels" but gave no further details. Possibly this observation involves a feeding activity.

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STRUCTURAL HABITATS OF WEST INDIAN *ANOLIS* LIZARDS I. LOWLAND JAMAICA

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ABSTRACT. This paper reports differences in structural and climatic habitat among the commonest *Anolis* species of three lowland Jamaican localities. Three of the species studied, *grahami, opalinus,* and *valencienni,* occurred at all localities; two other species, *sagrei* and *lineatopus,* occurred at one (Whitehouse) and two (Port Antonio, Mona) localities, respectively, and thus were complementary.

With a few exceptions, the ordering of species by height, from highest to lowest, was *valencienni, grahami, opalinus,* and *lineatopus* or *sagrei;* the ordering by diameter, from thickest to thinnest, was *opalinus, grahami, lineatopus* or *sagrei,* and *valencienni;* the ordering by insolation, from sunniest to shadiest, was *sagrei, grahami, valencienni, lineatopus,* and *opalinus;* the ordering by size, from largest to smallest, was *valencienni, lineatopus, grahami, sagrei,* and *opalinus.* Within species, larger individuals tended to occur higher and on thicker perches, smaller individuals lower and on thinner perches.

The above orderings result in low interspecific spatial overlap of similarly sized individuals in two ways. First, a *direct* relationship between body size and perch diameter *within* species and an *inverse* one *between* species ensures that spatially abutting species will overlap most their respective individuals least alike in size. Second, a direct relationship within species between size and height also, except for *valencienni* and *grahami,* results in the greatest spatial overlap being between the most dissimilarly sized individuals.

Many statistically significant associations were found between the habitat and climatic variables; the most common was a tendency for thin perches to be more often occupied in the sun.

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This is the first of a series of papers describing in a standard way the structural habitat of some West Indian *Anolis* lizards. Its primary purpose is to document differences between the size and sex classes of all the *Anolis* species found within a particular, limited study area. Between-site comparisons will be drawn occasionally; however, because of the great intersite variation in vegetation structure and its effect on lizard habitat distributions, that aspect will be described and analyzed in detail in a larger work covering much of the western Caribbean.

The "structural habitat," a term first invented by Rand (1964) for *Anolis,* refers to the spatial niche of a species population described in terms of characteristics of the vegetation and other structures upon which these arboreal animals carry out their activities. The two such characteristics that Rand originally used and that have subsequently proven most useful in discriminating the various species or species-classes are perch height and perch diameter (Rand, *l.c.,* 1967a; Rand and Rand, 1966; Schoener, 1968; Schoener and Gorman, 1968; Laska, 1970), and these will be the ones used below. Other possible structural characteristics are perch texture, perch color, and the size and nature of the plant or other object to which the perch is attached.

Observations that combine to give an overall picture of the spatial dimensions of the niche must be summed over a given time period and over a particular set of individuals. The method chosen in this and succeeding studies is to lump together "first sightings" recorded continuously throughout the day or throughout the period of maximum activity from a population of several hundred animals for each of the the commonest species. Thus, ideally, the sites of the major activities—thermoregulation, searching for food, capturing and eating prey, and social interaction—are weighted when observations are combined according to that fraction of the day spent by the average individual in the particular activity.

There are several limitations and qualifications of the structural-habitat concept which must be mentioned at the outset.

First, it does not provide a true picture of the animals' daily perch distribution, because inconspicuous animals are more often missed. This means that the most visible activities, feeding or fighting, for example, are disproportionately weighted in the totals. Inconspicuousness is perhaps less of a problem for continuous observation of single individuals than for "first sightings."

Second, weighting activities in proportion to the amount of time they take will not necessarily produce the most meaningful measure of a species' spatial distribution, either for testing hypotheses of optimal individual behavior or of community composition. For example, it may be most useful to know the places where prey are captured in order to determine how similar species can be and still coexist, but this activity consumes a very small amount of time, and Andrews (1971) and Trivers (personal communication) have both shown that distributions of feeding sites can differ markedly from the overall structural habitat. However, taxonomic breakdown of the prey of the four Bimini *Anolis* has shown that the prey is qualitatively what would be predicted from the overall structural habitat (Schoener, 1968).

Third, consideration of structural habitat alone provides an incomplete picture of the total niche of a species. The most important other kind of property characterizing the space in which an anole lives is climatic; some measure of this is given below for certain situations. A second important way in which animals of the same structural habitat may differ is in the prey selected from the habitat.

Fourth, structural habitat as determined by first sightings is a static concept: it says nothing about how an animal gets from one part of its home range to another, nor indeed about how perches of various heights and diameters are actually connected together in the habitat. Knowledge of the movements of animals is essential for certain kinds of studies, for example, those on foraging strategies, and may provide some indication of the type of prey captured. This limitation for Jamaican *Anolis* is important: Trivers (personal communication) has shown that *valencienni* differs strikingly from some other Jamaican anoles (e.g., *lineatopus*) in its active but cautious manner of searching for prey. The limitation should be kept in mind when *valencienni* is compared to the other species below.

Despite these disadvantages, the structural habitat has proven a useful "summary statistic" in describing *Anolis* communities. It has the great advantage that large populations of animals can be sampled quickly, thus permitting several such populations to be studied in a season. More balanced and detailed intralocality studies of *Anolis* populations are better for many purposes but are impractical for the study of the geographic variation of the niche. Hopefully, as greater numbers of these detailed studies

become available, it will be possible to set up correspondences—e.g., animals which are often found on leaves take large numbers of aphids—between the many properties measured in the detailed studies and the few properties of the overall structural habitat. Then some supposition can be made concerning the geographic distribution of many more species characteristics than those explicitly given as the "structural habitat."

FORMAT

The format for reporting the results in this and succeeding papers will begin with a description of the localities studied, including a list of the *Anolis* lizards seen. This will be followed by a verbal summary of the results for each locality, accompanied by tables depicting the structural habitat of the lizard classes considered, as well as by a table indicating the statistical significance of differences in the habitat variables between all possible pairs of the lizard classes. Finally, some relation will be made of the results to previous studies of the species in question and to studies of the habitats of species from other areas.

METHODS

Structural habitats were estimated by the "censusing" method first developed by Rand (1964). In a transect through the study area, each new lizard seen, unless obviously disturbed by the observers, is noted as to its perch height, diameter, and (sometimes) insolation. Rand (1964, 1967a) and Schoener (1968) have pointed out the possible errors in this technique, including the especially serious one of differential visibility of various portions of the habitat. Thus lizards, sitting, for instance, on the tops of leaves in the canopy, are often likely to escape detection. However, the *direction* of difference between lizard groups within a given site should not usually be affected by this kind of error. We did most of the observations as a pair, using binoculars, the two of us crisscrossing the habitat about 10 to 20 feet apart; this technique probably reduced considerably the chance of missing lizards. Study areas were often censused several times per day, but as a rule no part of the area was censused at intervals closer than one and a half hours; observation of lizard behavior in the interval indicates that this was ample time for the animals to "recover" from disturbance.

Data were cast into standard tables for easy intergroup comparison of structural habitat (Tables 1-4). For each lizard class for which microclimatic information was taken, observations of climatic categories—sun, shade, and clouds—were lumped into a single structural habitat table. Additionally, however, the percent occurrence in the three climatic categories were listed separately for each class (Table 5).

A powerful new technique of multivariate analysis was used to compute the statistical significance of habitat differences among the various groups of lizards. The technique utilizes the iterative procedure of Deming and Stephan (1940) and was recently expounded by Bishop (1969). It is designed to detect associations between variables—in our case perch diameter, perch height, lizard class, and insolation—of complex contingency tables; thus it can handle both nominal and ordinal variables. Because it also simultaneously considers associations between the habitat variables *per se,* this technique should largely eliminate any apparent difference in habitat among lizard classes caused entirely by the structure of the vegetation. For example, were relatively high perches always also relatively thin perches, a lizard class which occupied significantly higher perches, in the statistical sense, would not necessarily occupy significantly thinner perches, because of the strong height versus diameter interaction. Details of the application of the method to our data are given in the appendix (see also Schoener, 1970). The reader not familiar with these techniques should first consult the paper by Fienberg (1970), which is an exposition of the method written especially for ecologists.

THE SPECIES

There are seven species of *Anolis* described for Jamaica (Underwood and Williams, 1959).

Two of the species—*sagrei* and *grahami*—can be characterized as inhabiting strictly lower and middle elevations. *A. grahami* is very widespread, occurring abundantly throughout the lowlands. Typical *grahami* (subspecies *grahami*) are medium-sized (♂ snout-vent length (SVL) = 65.5 mm; ♀ SVL = 44.0 mm)[1] green to

[1] Means are of the largest third of all specimens examined (see Schoener, 1969).

green-blue lizards occurring in all areas but the northeast, where they are replaced by *grahami aquarum,* a somewhat smaller (♂ SVL = 61.8 mm; ♀ SVL = 45.1 mm), bright emerald green lizard. *A. sagrei,* a medium-small (♂ SVL = 50.4 mm; ♀ SVL = 40.9 mm) brown species, is restricted in habitat on Jamaica, occurring only over the western portion of the island and there confined to the openest, sunniest areas. It is often associated with rocks. Apparently, *sagrei* has invaded Jamaica from Cuba and is in the process of spreading eastward (Underwood and Williams, 1959; Williams, 1970).

Another primarily low and middle elevation species is *lineatopus.* This medium-sized (♂ SVL = 62.7 mm; ♀ SVL = 43.6 mm) lizard is perhaps the most varied in its coloration and pattern: four subspecies are recognized, some of which are found in dry open areas and others of which are restricted to the darkest forest (Underwood and Williams, 1959).

Two species have been recorded from the lowlands to *c.* 4500 feet. *A. opalinus,* slightly smaller than *sagrei* (♂ SVL = 49.5 mm; ♀ SVL = 40.5 mm), comes in varying patterns and shades of brown and grey. There is scarcely a locality in Jamaica that does not have this species, though in the lowlands it is restricted to the shadiest areas and in the uplands is found in very open situations (Underwood and Williams, 1959; Rand, 1967; this paper). The grey-white, medium-large (♂ SVL = 79.4 mm; SVL = 68.5 mm)♀ *valencienni* seems not to reach the density that the aforementioned species sometimes do but is found throughout Jamaica, including some areas above 4000 feet. It appears to be commoner in open than in heavily shaded situations, but by no means is absent from the latter (see below).

The above five species are the ones which occurred commonly at one or more of the three localities studied, and which are therefore included in the comparisons to follow. A sixth species, the "green lizard" *garmani,* was seen at each of the three study sites, but rarely. It is the largest of the Jamaican anoles (♂ SVL = 110.0 mm; ♀ SVL = 82.5 mm) and occurs throughout the island at all elevations (Underwood and Williams, 1959). However, it is most abundant relative to other *Anolis* species at middle elevations (*e.g.,* Trivers, MS, and below), though it is also known to be common at certain lowland localities, such as the "ironshore" vegetation along the northwest coast. The seventh species, *reconditus,*

is restricted to middle and upland elevations and has only recently been discovered (Underwood and Williams, 1959; Lazell, 1966).

LOCALITIES

Three lowland localities were selected for study, representing a wet, a rather dry, and a mesic area.

The first, about ten acres in extent, was located east of the town of Port Antonio, on Jamaica's northeast coast. Specifically, it extended over the northwestern edge of a point of land supporting the ruins of an estate locally referred to as the "Folly." The vegetation was quite secondary: planted trees and shrubs, such as *Ficus,* limes, palms, and mango trees intermingled with native vegetation such as *Terminalia.* This locality had, however, become considerably overgrown, and there then existed, side-by-side, an area of almost continuous canopy and oftentimes sparse understory on the one hand, and an area of widely spaced trees and shrubs with much low, tangled herbaceous vegetation on the other. Both areas were studied and will be discussed separately as "Port Antonio Open" and "Port Antonio Closed."

The locality was worked 30 June–11 July 1967. Despite the fact that Jamaica was then undergoing one of its most intense droughts, rain fell fairly frequently though not protractedly; the area averages 131 inches of rain per annum (Handbook of Jamaica, 1966). The anoline species *grahami aquarium, lineatopus lineatopus* (or intermediates betwen *lineatopus* and *ahenobarbus*) and, to a lesser degree, *opalinus* and *valencienni* were abundant in the open area; the species *opalinus* and *lineatopus,* and to a much lesser degree *valencienni,* were common in the closed area.

The second study site, about four acres in extent, was located at Mona, near Kingston, in tall, open forest near the base of Long Mountain. It apparently was marginal to Rand's (1967) "Mona bush" study area, but differed in its much greater preponderance of *grahami.* Vegetation in this area consisted of large trees and smaller woody shrubs of typical tropical dry forest aspect: thorns, flattened canopies and small, numerous leaves. The understory, in addition to the shrubs, was mostly grass of about one to two feet in height, but certain patches were practically cleared while others had a more varied herbaceous vegetation. The latter appeared seriously affected by the drought. The site in general falls within Asprey and Robbins' (1953) "dry limestone scrub forest."

The area was studied 13-18 July 1967. Rainfall was almost nonexistent during this period. The nearby Hope Gardens record 51 inches of rain per year (Handbook of Jamaica, 1966), though because of the extreme microgeographic variation in climate found on the Greater Antilles, this figure may not be the same as that for the study site itself. The anoline species *grahami grahami, lineatopus lineatopus* and *opalinus* abounded in the area. In addition, *valencienni* was not uncommon.

The third study area was located about one mile west of Whitehouse, near the southwest coast. It consisted of groups of trees and shrubs of mesic to xeric aspect, which remained after partial conversion into pastureland. The portion of this area closest to the coast was planted in limes and pimentos; further upland, patches of native trees merged gradually into unbroken forest. In places, considerable grassy and rocky areas showed effects of heavy grazing. The vegetation is labelled by Asprey and Robbins (1953) "cultivated pasture or second growth scrub," bordered by remnants of "dry limestone scrub forest," or by forest transitional between that and "wet limestone forest." The total area considered encompassed about 15 acres, though parts of it were not included in the censuses.

The area was studied 21-27 July 1967. Weather was regular and cyclical during that time, sunny mornings giving way to overcast or partly cloudy afternoons, accompanied sometimes by heavy downpours. A nearby town (Bluefields) logs 91 inches of rain per annum (Handbook of Jamaica, 1966). The form *grahami grahami* occurred throughout the study area. The other two common species, *sagrei* and *opalinus,* were restricted to open and closed areas respectively, and their horizontal ranges, though interdigitating, overlapped little at the same time of day. A fourth species, *valencienni,* was seen rarely. The investigation of the *opalinus-grahami* area has been partly reported in a different context (Schoener, 1970) but will be reiterated in entirety below so as to standardize its results.

RESULTS FOR LIZARD STRUCTURAL HABITATS

In the following discussion, all comparisons, unless stated otherwise, are statistically significant (Tables 6-9) as judged by the technique described in the appendix. Statements in the text to follow, such as lizards of species A "occurred higher" or "were

higher" than those of species B, should be interpreted as descriptive of the modal individual or the bulk of the population rather than of all individuals in the species' population. Large lizards could always be distinguished as adult males and will generally be referred to hereafter simply as "males." Smaller lizards included mostly adult or subadult females but also included some subadult males; they were all lumped into the class "female-sized lizards" because they could not usually be distinguished in the field. When sufficiently abundant, the smallest lizards—"juveniles"—are considered separately.

Mona (Tables 1, 6). At Mona, ten classes of lizards in four species were considered.

The highest lizard species observed was *valencienni:* males occurred higher than any other class, and female-sized *valencienni* were higher than all but *grahami* males. *A. grahami* was the next highest species: its males occurred higher than all classes of *lineatopus* and *opalinus.* The males of *opalinus* occurred higher than female-sized *grahami* and all *lineatopus.* Female-sized *grahami* were higher than all *lineatopus* and female-sized *opalinus.* Male *lineatopus* occurred higher than female-sized *opalinus* and *grahami* juveniles. Female-sized *opalinus* occurred higher than *grahami* juveniles and female-sized or juvenile *lineatopus.* Juveniles of *grahami* were higher than female-sized and juvenile *lineatopus.*

A. opalinus as a species was on perches of the greatest diameter; males of this species were on significantly thicker perches than all classes but male *grahami,* and only the latter occupied thicker perches than female-sized *opalinus.* Male *grahami* were also on thicker diameters than any other interspecific class. Female-sized *opalinus* and male *lineatopus* had about the same perch diameters but were on thicker perches than *valencienni* and female-sized or juvenile *grahami* and *lineatopus.* Female-sized *grahami, valencienni,* and *lineatopus* all occurred on thin perches of nonsignificantly different diameter. Juveniles of *lineatopus* and *grahami* occupied the smallest perches, the latter the smallest of all.

Intraspecifically, in all four species males perched higher than did female-sized individuals, and female-sized individuals in *grahami* and *lineatopus* occurred higher than did juveniles. In all but *valencienni,* males frequented thicker perches than did female-sized individuals, and in *grahami* and *lineatopus,* female-sized lizards were on thicker perches than juveniles.

Although climatic observations were not recorded at Mona, our impression is that the species tended to separate the way Rand (1967a) has described for a nearby area: *grahami* and *valencienni* were in the openest, sunniest situations; *lineatopus* was intermediate; and *opalinus* was in the shadiest areas. Relatively shady areas at Mona are associated with large-diametered trees, and the comparatively small *opalinus* preferred trees

whose diameters were bigger than those for any group but *grahami* males.

Port Antonio Open Area (Tables 2, 7). The classes studied in the open segment of the Port Antonio site were the same as those observed at Mona.

In relative height, the lizard classes were arranged in nearly identical fashion to those at Mona. Male *valencienni* were the highest, as before, followed by *grahami* males, which were here significantly higher than female-sized *valencienni*. Probably the greater number of low thin-branched shrubs in relation to trees in the open area at Port Antonio is responsible for this discrepancy with the Mona area. Next in height were male *opalinus*, higher than female-sized and juvenile *grahami* as well as all classes of *lineatopus*. Female-sized *grahami* and *opalinus* were distributed over similar heights and were higher than any class of *lineatopus*. Males of *lineatopus* were higher than juvenile *grahami*, but the latter were higher than female-sized or juvenile *lineatopus*.

In diameter, there was a major reversal from the pattern at Mona. Adult male *valencienni*, the largest of the four species, occurred on diameters not significantly thinner than those of *grahami* or *opalinus* males and significantly thicker than those of male *lineatopus*. Males of *opalinus* at Port Antonio were on thicker diameters than *grahami* males, and the latter showed no significant difference from female-sized *opalinus*. Female-sized *opalinus* were on thicker perches than female-sized or juvenile *grahami*, *lineatopus*, or *valencienni*. Males of *lineatopus* occurred on larger-diametered perches than did female-sized and juvenile *grahami* or female-sized *valencienni*. Female-sized *grahami* occupied thicker perches than did female-sized *valencienni* or female-sized and juvenile *lineatopus*. Female-sized *valencienni* occurred on thicker perches than did female-sized *lineatopus* or juveniles of *grahami* and *lineatopus*. Finally, female-sized *lineatopus* were on thicker perches than *grahami* juveniles.

Within the same species, males of *grahami*, *opalinus*, and *lineatopus* were found higher than smaller-sized individuals. In addition, female-sized anoles were higher than juveniles in *grahami* and *lineatopus*. For each species, classes whose individuals were of the largest size were found on thicker perches than all classes of smaller individuals.

Once again, *opalinus* and *grahami* segregated by shade and sun, respectively. And again, *opalinus*, a small species, occurred on bigger trunks and branches than did the larger species *grahami* or *lineatopus*. *A. opalinus* was also found close to the ground in shrubby, more tightly packed vegetation, where it was able to perch in the shade. In such areas, which were scattered in patches throughout the study site, *grahami* ranged higher, being found on leaves and more exposed branches. As at Mona, male *lineatopus*, similar in size to male *grahami*, were more often found on thinner perches.

Unlike the Mona situation where leaves were mostly small, the Port Antonio site contained many broad-leaved herbaceous plants. In such vegetation, particularly on leaves, it was common to see female and juvenile

grahami (Table 2). It is possible that *aquarum,* which is that form of *grahami* inhabiting the wettest lowland areas (including Port Antonio), is both smaller and of a brighter, more leafy green color because of its opportunity for occupying the more luxuriant green vegetation resulting from the heavy rainfall.

Port Antonio Closed Area (Tables 3, 8). In this more shaded site, so few *valencienni* were seen that they are all lumped into one category. Representatives of *grahami* were also very uncommon and are therefore not included. In addition, because of the much greater abundance of *opalinus,* female-sized individuals are treated separately from juveniles in that species.

In height, differences between all possible pairs of lizard classes were significant. The order of groups, from highest to lowest, was *valencienni, opalinus* males, *lineatopus* males, female-sized *opalinus, opalinus* juveniles, female-sized *lineatopus,* and *lineatopus* juveniles.

In diameter, *opalinus* males were on thicker perches than any other group. Female-sized *opalinus,* male *lineatopus,* and *valencienni* occurred on perches not significantly different in diameters, and all were on thicker perches than female-sized *lineatopus* or juveniles of *opalinus* and *lineatopus.* Female-sized *lineatopus* occurred on thicker perches than did juveniles of *opalinus.*

Intraspecific relations paralleled those for the other two areas: in *opalinus* and *lineatopus,* the larger the size of the lizard, the higher it occurred, and the thicker were its perches.

Whitehouse (Tables 4, 9). The study site near Whitehouse is identical in species composition to those near Mona and Port Antonio except that *sagrei* replaces *lineatopus.* The only form of *lineatopus* in the vicinity of the site is *neckeri,* an animal which seeks darker forest than *opalinus.* As stated above, climatic observations were recorded at Whitehouse in addition to those on structural habitat. Although reported in part elsewhere (Schoener, 1970), data treatment here differs in two major respects: the category "clouds" was added to those of "sun" and "shade" for the climatic variable, and "time" is not considered as an additional variable.

In this area again, *grahami* males and *valencienni* (all classes combined) were found at the greatest heights. They were followed by female-sized *grahami,* which occurred higher than any class of *sagrei* or *opalinus.* Juvenile *grahami* were found higher than *sagrei* and male *opalinus.* Both classes of *opalinus* perched at greater heights than did any class of *sagrei.*

Male *grahami,* male *opalinus,* and female-sized *opalinus* did not show significant differences in perch diameter, though the first were on the thickest perches. Male *grahami* were found on thicker diameters than male *sagrei,* but the latter did not differ significantly from either class of *opalinus.* Male *sagrei* occurred on thicker perches than did female-sized *grahami,* juvenile *grahami* and *valencienni.* Female-sized *sagrei,* juvenile *sagrei* and *valencienni* all had greater-diametered perches than did juvenile *grahami.* In addition, *sagrei* juveniles perched at greater diameters than did the combined *valencienni.*

Within the same species, adult males of *grahami, sagrei,* and *opalinus* perched higher than female-sized individuals. The latter in *sagrei* perched higher than juveniles, but in *grahami* the two classes were similar in height.

Once again, males of the three commonest species occurred on thicker perches than did smaller individuals, but the results were not significant for *opalinus.* Juveniles in *grahami* and *sagrei* were found on thinner perches than the other intraspecific classes.

Although there was an overall tendency for *sagrei* and *valencienni* to be found most often in the sun and *opalinus* most often in the shade or on cloudy days, this pattern varied by species class (Table 5). Males of *opalinus* were most consistently found in the shade: they were seen significantly more often during cloudy days or occurred more often on shady perches than male and juvenile *sagrei,* male and female-sized *grahami,* and *valencienni.* Juveniles of *sagrei,* in contrast, were very frequently seen in the sun: all classes of *grahami* and male *opalinus* were seen significantly more often in the shade or during cloudy weather than were juvenile *sagrei.* Only two other intraspecific comparisons were significant: female-sized *grahami* were most often seen in the sun or during cloudy days than male *sagrei,* and *valencienni* were most often seen in the sun or on cloudy days than male *grahami.* Thus there was no invariant tendency for that class recorded most often in the shade to be also the one recorded most often during cloudy weather.

Only a few intraspecific differences were significant: male *opalinus* were recorded more frequently in the shade or on cloudy days than smaller *opalinus;* female-sized *grahami* were more frequently seen in the sun or on cloudy days than male *grahami,* and female-sized *sagrei* were more frequently seen in the shade or during cloudy weather than juvenile *sagrei.* Thus there was some inclination for the smaller-sized lizards within a species to be on sunnier perches.

DIFFERENCES BETWEEN HABITAT VARIABLES

The statistical treatment of the structural-habitat data also detects significant interactions between the two perch variables, height and diameter, and when available, the climatic variable. Thus it answers the following kind of question: is there a significant association between thin perches and high perches for all perches combined of the two lizard classes being compared?

At Mona, for most comparisons among lizard classes, small perches occurred at greater heights than did large perches (Table 6). However, in the three of nine cases in which a significant height-diameter interaction was found (male *grahami* with female-sized *grahami,* male *valencienni,* or female-sized *valencienni*), the

reverse was true. In the Port Antonio open area, on the other hand, where trees were more widely scattered and there was much low second growth, all significant associations were of small-diametered perches with low heights. Whitehouse resembled the Mona area more than Port Antonio in its relation of perch height to perch diameter; low perches tended to be of larger diameter. This interaction again reflects the vegetation structure: at Whitehouse, there were few tall trees and little herbaceous understory—most large perches were therefore low, including the fenceposts especially preferred by *sagrei*. The only statistically significant exceptions to this pattern were for *sagrei* juveniles, the most terrestrial class of lizards on the site.

At Whitehouse, it was also possible to look for associations between the climatic categories and those of perch height and diameter (Table 9).

There were few significant interactions between perch height and insolation, probably because, in the patchy vegetation of the study site, the sun penetrated for the most part to vegetation of all heights. For intraspecific *sagrei* comparisons, higher perches tended to be relatively shady and lower perches relatively sunny. Individuals of *sagrei* were found more often than those of other species in areas away from the shade provided by large trees and shrubs: in such areas, most perches are both low and sunny. Lower perches in sun than during cloudy weather were found for the combined data of juvenile *grahami* and male *sagrei*. In contrast, the lowest perches were found in the shade or sun and the highest on cloudy days for female-sized *sagrei* lumped with *grahami* males. Why these were the only interspecific comparisons showing a significant height-insolation interaction is not apparent.

There were many more significant associations between perch diameter and insolation. All but one were of two sorts: the thinnest perches were occupied in the sun and the thickest in either shade or on cloudy days. (The exception was for female-sized and juvenile *grahami:* thinnest perches were shadiest, and thickest perches were utilized during cloudy weather.) In a previous study which also separated observations by time of day, a three-way interaction between diameter, insolation, and time was detected at Whitehouse (Schoener, 1970). Exterior perches tend to be thinner in all habitats, but in patchy ones such as that at Whitehouse, tend to be sunnier as well—thus the association may simply reflect the physiognomy of the vegetation. However, Jenssen (1970) found that

individuals of *Anolis nebulosus* climb into vegetation during midday and has attributed this behavior to a warming of the substrate. Perhaps a similar thermoregulatory function can explain the lizards' avoidance of sunny, large surfaces during most of the day at Whitehouse.

In several of the comparisons for each locality, the statistical procedure indicated that there might be significant three-way interactions between the variables (see appendix). Several are of interest. Two were interactions between perch diameter, insolation and lizard class. These were cases in which a low class, one of *sagrei,* was paired with a higher class, one of either *grahami* or *valencienni.* In *sagrei,* thick perches are more likely to be used in the shade on sunny days, whereas in the more arboreal forms, thick perches are more likely to be used on cloudy days. Another three-way interaction showed that *sagrei* males tended to seek out shady perches that were most often relatively high, whereas female-sized *sagrei* found their shady perches relatively lower. Both these results probably reflect differences in regard to relative availability of sunless perches between the habitats of the classes being compared.

As inspection of Tables 6-9 shows, there is a considerable number of significant interactions involving climatic and/or habitat variables alone; therefore the extended statistical treatment given the data of this paper is well justified. Most of these interactions reflect differences in the vegetational structure and its exposure to the sun. As mentioned, a few may indicate thermoregulatory behavior on the part of the lizards. However, the use of the climatic categories—sun, shade, and clouds—can only give a crude first approximation of the climatic preferences of these animals. Finer resolution would be gained were temperature, humidity, wind speed, and other variables measured at each perch.

DISCUSSION OF LIZARD STRUCTURAL HABITATS AND RELATION TO PREVIOUS STUDIES

The climatic and structural habitats of the lowland species can be summarized as follows.

1. *Climatic.* As first pointed out by Rand (1967a) for Kingston populations, in all localities *grahami* inhabited relatively open, sunny places and *opalinus* relatively closed, shaded places. At Mona and Port Antonio, *lineatopus* was intermediate in this regard. However, *sagrei,* its structural habitat counterpart at Whitehouse, occurred in sunnier, more exposed places than did *grahami.* In that

locality, *opalinus* occurred on lower perches than elsewhere and thus occupied in part perches where *lineatopus* would have been expected were it present.

2. *Structural.* In all four study areas, *valencienni* as a species was seen higher than its congeners (Figs. 1-4). Wherever found, *grahami* was next in height, followed usually quite closely by *opalinus*. However, at Port Antonio female-sized lizards of *grahami aquarum* were lower than either class of *opalinus,* reflecting their abundance in herbaceous vegetation at that site. *Lineatopus* and *sagrei* both occurred lowest in their respective sites though *sagrei* appeared relatively more terrestrial. The ranking of species by height at Mona was the same as that found by Rand in several localities near Kingston. As can be seen from the figures, no particular between-species relationship of species-size to height was evident. However, within species, smaller lizards always tended to occur lower than did larger ones.

The ordering of species with respect to perch diameter is slightly less consistent from locality to locality. At Mona, both male and female-sized lizards taken separately showed a perfect inverse relation of body size and perch diameter: the largest species, *valencienni,* occurred on the thinnest perches, followed by *lineatopus,* then *grahami,* and finally, the smallest species, *opalinus* (Fig. 1, Table 1). At Port Antonio Open, the situation was the same except that male *valencienni* occurred on thicker perches than all but male *opalinus,* and female-sized *lineatopus* occurred on thinner perches than female-sized *valencienni* (Fig. 2, Table 2). At Port Antonio Closed, where only two species were considered in detail, *opalinus* again took thicker perches than did *lineatopus* for both sexes (Fig. 3, Table 3). At Whitehouse, the ordering was essentially the same as at Mona, except that *sagrei* replaces *lineatopus* (Fig. 4, Table 4). However, *sagrei* is smaller than *grahami,* so there is not a perfect inverse relation of species-size and diameter at Whitehouse. Taken as a whole, the data are in almost total opposition to what would be expected if perch diameters were selected by species on the basis of body weight.[1] The inverse relation is made all the more interesting by the fact that within each

[1] It should be pointed out, however, that *garmani,* the largest species on Jamaica, was very rare and was therefore not considered in the study sites. What few data exist on the perch diameter of this species (Rand, 1967a, our unpublished data) indicate that *garmani* do not inhabit thinner perches than *valencienni* but rather are often found on large trees and therefore often perch on large branches.

species, all significant associations are of larger individuals with larger perches and vice-versa. Clearly some explanation other than a purely supportative one must be sought for species-specific differences in perch diameter.

A possible explanation is the following. Given that, within species, larger individuals are found on larger perches, an inverse relation between perch diameter and species size would be expected if species evolved so that that class of a given species overlapping in space the most with a class of another species was the one which differed the most in size from the latter class. In other words, a direct relationship between size and perch diameter *within* species and an inverse one *between* species is one way of ensuring that interspecific spatial overlap is between dissimilarly sized individuals. In fact, given the direct, within-species relationship, none of the 24 possible permutations of the species ordered by diameter results in less total difference in the sizes of the most closely overlapping interspecific pairs, though a few alternatives are about as good as the one discussed. Because anoline lizards of different sizes take differently sized foods (Rand, 1967a; Schoener, 1967, 1968; Schoener and Gorman, 1968), such staggering of sizes in space should alleviate resource competition (Rand, 1967b; Schoener, 1968).

Reversal of *both* the within- and between-species relationships is, of course, an alternative way of juxtaposing dissimilarly sized classes from different species. Why then does this second arrangement not occur instead? An answer can perhaps be found if we examine the probable course of faunal increase on Jamaica. It is highly unlikely that the four species evolved simultaneously and sympatrically. Therefore, while in isolation from other anoles, the first species to have evolved probably showed a *direct* within-species relationship between body size and perch diameter: not only is a direct relationship adaptive over the large range in body sizes spanned by the different age classes, but dominant individuals in *Anolis* are usually largest (Rand, 1967b; Trivers, in prep.; Schoener, in prep.) and would therefore appropriate the most suitable perches. Furthermore, all solitary species studied in heterogeneous vegetation showed such a direct relationship (Rand and Rand, 1966; Schoener, 1967; Schoener and Schoener, in prep.). Upon coming together, in order to achieve the second arrangement, the species would have to change their species-specific size and/or

perch diameters *as well as* the within-species relationship between size and perch diameter. Rather than that, it seems more feasible for species to shift their size and/or perch diameters in such a way as to preserve the intraspecific relationship and still avoid overlap of similarly sized individuals, *i.e.,* in accordance with the existing arrangement. The positioning of a relatively large species on perches of relatively small diameter could then be facilitated by morphological changes in body proportions, such as those in relative leg length. Indeed, some proportional differences do seem to exist in the Jamaican species: *valencienni,* the largest species considered, has relatively short limbs, particularly in femur. Similar changes in proportions would likely be more difficult to build into the ontogeny of single species, as would be necessary were the second arrangement adhered to.

Though there is no between-species relationship of perch height and size, the within-species tendency for smaller individuals to be found relatively low also results in minimal interspecific spatial overlap of similarly sized individuals, except for the *valencienni-grahami* combination, in which female-sized *valencienni* are about the same size as male *grahami.* However, those classes occur on quite different perch diameters (Figs. 1-2, Tables 1-4), and Trivers (personal communication) has evidence for major differences in searching for prey and, possibly, prey taxa between the two species. Rand (1967a) noted a tendency for *opalinus* and *lineatopus* to juxtapose dissimilar sizes according to height, in localities around Kingston, but he found the opposite for *grahami* and *lineatopus.* A further difference between Rand's and our study is that his data for small-sized *grahami* are bimodally clustered by height, one mode being below six feet and the other above ten feet. A likely reason for the discrepancy is difference in the structure of the available vegetation of the respective sites. Rand observed most of his *grahami* on the campus of the University of the West Indies where there is little high, shrubby understory surrounding the large trees. Thus the distribution of female-sized *grahami* may have paralleled differences in vegetational layers. The three localities we looked at were all more overgrown and vegetationally more heterogeneous. We also found a greater difference in perch height between male and female-sized *grahami* in all localities than did Rand. Possibly at Mona there were many more females on high branches than we were able to detect, but this is unlikely to be much of a factor at

either Port Antonio or Whitehouse, where the canopy is lower and more broken. Again, the lack of a viney, bushy understory in the "park-like" vegetation where Rand studied most of his *grahami* is probably responsible for the difference. A third possible reason for the difference is simply some effect associated with the smaller sample size Rand used, either one purely of sampling error, or one related to a smaller range of times of day or weather conditions than covered in our study.

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APPENDIX I

Statistical Appendix

Data of the sort presented above are ideally treated in the form of a multiway contingency table, because variables are both ordinal (perch height and diameter) and nominal (lizard group, climatic category). In the case of nominal variables, there is no problem in selecting categories (referred to as "levels"): there are two lizard groups and three climatic categories (see above). However, for ordinal variables, a continuous set of quantitative data must be broken at one or more places in order to form categories. Because of the multiplicative increase in the total number of cells in a contingency table with increasing number of categories for a single variable, two categories each were chosen for perch height and perch diameter. That is to say, all observations less than or equal to some number were cast into one category, and all those greater than that number were cast into the other. The point at which the data were broken was chosen by computing that number which gave the maximum difference in cumulative frequency between the two distributions of observations belonging to the lizard groups being compared. Hence this procedure was designed to detect

maximum differences in height and diameter taken separately between the lizard classes, although because of interactions between variables, it will not necessarily produce a maximum difference in a combined model. The critical values were, of course, usually much removed from those required to give maximum interaction between the environmental variables themselves (e.g., perch height and insolation). The critical value so determined for height or diameter was generally different in different comparisons, and ranged from one-fourth inch to four inches for diameter and eleven inches to ten feet for height. An alternative procedure would have been to choose the same intervals for all comparisons, but given the great variation in lizard habitat preference, would have obscured most differences. What we have in effect done is to redefine "high" and "thick" for each comparison. There are statistical objections to this procedure, but at present appropriate alternative methods of grouping data are not available (Fienberg, 1970). The points at which the data were broken are listed here (Table 10) for two reasons: 1) Other researchers may wish to define "high" and "thick" differently and therefore can better compare their method with the one used here; and 2) It is of biological interest when comparing habitat distributions to know where the point of maximum difference lies, especially in case the observations were repeated later in the same or similar areas.

Once categories were chosen, the procedures diverged for three and four variable situations.

In the four-way case, a contingency model was first set up which contained all possible two-factor or pairwise interactions between the four variables; in this case there were $\binom{4}{2} = 6$ such interactions. Then an iterative procedure described elsewhere (Bishop, 1969; Mosteller, 1968; Fienberg, 1970; Schoener, 1970) was used to fit the data to the model, that is, to compute expected values for each cell of the contingency table. Two measures of goodness of fit, the standard chi-square and the log-likelihood chi-square (Kullback, 1959) were computed and degrees of freedom determined as described by Ku and Kullback (1968) and Fienberg (1970). It was then noted whether the model gave a fit satisfactory at the 5 per cent level. In most cases the two statistics were very similar, but where they allowed a different conclusion to be drawn about significance, the log-likelihood ratio chi-square was followed.

Next, each two-way interaction was individually dropped, giving six new models. For each of these, the difference between the new

model and the original model was evaluated for statistical significance by testing the difference in their log-likelihood ratio chi-squares, according to the partitioning technique expounded in Kullback (1959), Ku and Kullback (1968), and Fienberg (1970). If all new models were significantly different from the old model at the 5 per cent level the process was terminated. Otherwise, that new model was then chosen (and thereby the corresponding interaction removed) whose log-likelihood ratio chi-square was most similar to that of the original model. The procedure was then repeated, five new models each containing four two-way interactions being tested against the model containing five two-way interactions. Interactions were thus removed, one at a time, until all models with a smaller number of interactions were judged significantly different from the next most inclusive model, or until no interaction remained.

Because of space limitations, detailed results could not be reported as they were in a previous paper (Schoener, 1970). Instead, the results are summarized in Table 10. The six tiers of the table correspond to the six possible two-way interactions. For each lizard combination, these are given a number from zero to four. A "1" denotes that the interaction remained significant in the above sense every time it was tested in the removal procedure. A "2" denotes that the interaction was significant at least at the termination of the procedure. A "3" means that the interaction was significant when removed from the most inclusive model (with six interactions) but not at termination. A "4" indicates that the interaction was significant sometime during the procedure but not at the beginning or end. A "0" indicates that the interaction was never significant. Interestingly, in Table 10 most interactions could be labelled either "0" or "1", and in the simpler three-variable case, all interactions could be so labelled (Tables 7-9). In the discussion of the text, any interaction labelled 1-4 is considered significantly non-zero, but the tables should be checked for fine distinctions.

In the case of three-variable tables (perch height, perch diameter, and lizard group), there are $\binom{3}{2} = 3$ two-way interactions. The reduction procedure for these was similar to that described for four-way tables, but of course is much shorter: only three new models need be tested against the most inclusive model on the first round instead of six.

Rarely, a set of models was encountered which never gave a

chi-square value denoting a satisfactory fit of the model at the 5 per cent level, regardless of what interactions were removed. These are labelled in the tables. In such cases, differences between models were still computed in the usual way and the results listed in the tables. In addition, however, a search was programmed for significant three-way interactions, in order to see if an improved fit could be obtained. In the case of four variables, there are $\binom{4}{3} = 4$ three-way interactions. The procedure was to test each of four models corresponding to the addition of a different three-way interaction to the model with all two-way interactions. For the Whitehouse data, there was no tendency for any particular three-way interaction to predominate: each produced the best fit at least once. Some of these are discussed in the text. In no case was it necessary to consider more than one three-way interaction in order to produce a satisfactory fit. Once such a fit was obtained, the three two-way interactions able to be removed were deleted one at a time as before, and differences in chi-square with more inclusive models were tested. In most cases, the two-way interactions that could be removed without producing a significant difference between models were the same as some of those removed in the analysis of two-way interaction models only.

In the case of a model with three variables, there is but a single three-way interaction. Fitting this interaction would be a trivial exercise resulting in a perfect fit (within the limits of computational accuracy); therefore, three-way interactions could only be considered for tables with four variables.

In several cases it happened that margins (the total number of observations in a particular category of a variable or combination of such categories) were zero. For these cases, two procedures were tried. The first was to correct for the additional degrees of freedom lost in such a table according to the method of Bishop (unpublished thesis; Fienberg, personal communication). Once this was done, the removal procedure could be carried out as before. In no case in the present study was the recalculated number of degrees of freedom zero or negative, though if there are too many zeros this will happen. A second way to handle zero margins is to adjust the table slightly by shifting one (if possible) or more observations so that margins are no longer zero. This is best done conservatively, that is, so as to reduce the likelihood of achieving a significant difference to the variables of interest, in our case those

in structural habitat. For such tables, where there was a choice from several cells for selecting the observation to be moved, the cell with the most observations was chosen. While far less preferable than the first method, table adjustment had to be carried out for the three-variable case, because the initial $2 \times 2 \times 2$ model tested has, assuming no zero margins, but one degree of freedom; thus no further deletion is possible. Unless otherwise specified, values in the tables of significance for four-way comparisons are computed by the first method, though in only about 15 per cent of tables with zero margins so far examined did conclusions from the two methods differ at all.

APPENDIX II

Remarks on Other Localities

Jamaica, like the other Greater Antilles, is large and topographically diverse, yet it contains only seven species as compared to Puerto Rico's ten, Hispaniola's 24 and Cuba's 24. Jamaica's less diverse fauna is in part apparently associated with a great variation from locality to locality within Jamaica in regard to what species are found in certain segments of the vegetation. Brief visits which we made to other Jamaican localities give an inkling of this variability. Already shown is that in western Jamaica *sagrei* replaces *lineatopus* as the open-area trunk-ground lizard. In darker, mesic forests west of the Whitehouse locality (such as that near Ferris Cross), the trunk-ground species is *lineatopus neckeri,* an olive green-brown form somewhat smaller than the nominate subspecies. *A. opalinus* is also common in such forests, but inhabits less shady places and is more likely to be encountered marginally. *A. grahami* seems entirely absent from these dark forests, but *garmani* is present. More xeric forests two to five miles east of the Whitehouse study area contained no trunk-ground species *per se.* Instead, *opalinus* occurred often on low perches (though no measurements were made), and *garmani* seemed commoner than at any of our study areas.

Yet other species combinations are possible. In natural beach vegetation near Rose Hall on the northwest coast, we saw *grahami* and *sagrei* commonly. Where this vegetation met the xeric "iron-shore" limestone formation, these species were replaced by *lineatopus merope,* a rubiginous form well camouflaged on the rust-colored limestone, and *garmani.* In certain moist mid-elevation sites such as

can be found about Mandeville, *garmani* was the common arboreal species, and *opalinus* occurred in quite open, sunny places, including low woodpiles and fenceposts. In these localities we found *grahami* to be practically absent, while *lineatopus neckeri* was common in the blackest part of the forest. E. E. Williams and T. A. Jenssen (personal communication) have also observed *opalinus* in exposed situations at Mandeville; Williams, however, found *grahami* moderately common in certain of these situations. In montane forest (*c.* 4000 feet), such as that surrounding Green Hills, we frequently observed *opalinus* in extremely exposed places, including along roadsides as at least temporarily a terrestrial lizard. Other lizards in the area were *valencienni* in open situations and *garmani* in somewhat more enclosed places; we also saw several *reconditus* in relatively dark woodland.

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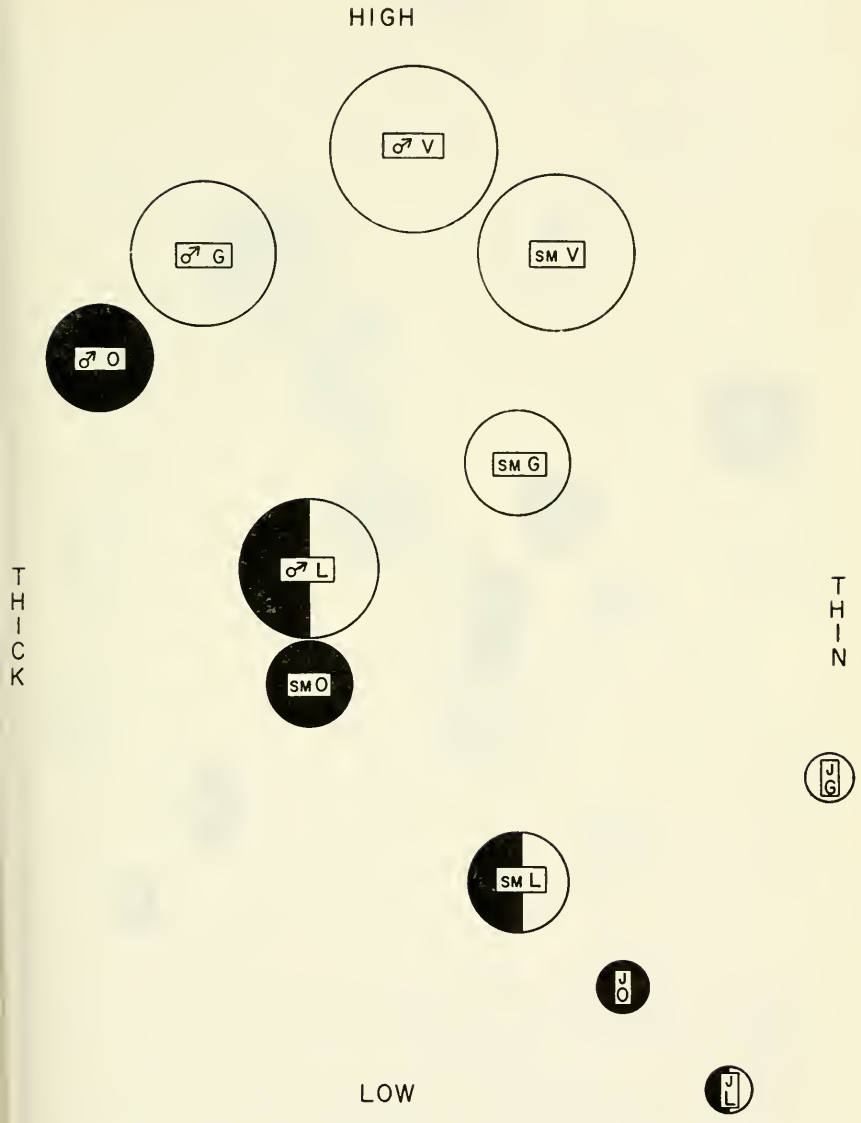

Figure 1. Mona. Species-classes are ranked by perch height and perch diameter; distances between species-classes are not representative of the magnitude of difference. Circles have diameters in proportion to the length of the individuals in the designated class. Clear circles are of classes found mostly in open, sunny areas; shaded circles are of classes in mostly closed, shady situations; intermediate classes are represented by half-shaded circles. V = *valencienni*, G = *grahami*, O = *opalinus*, L = *lineatopus*.

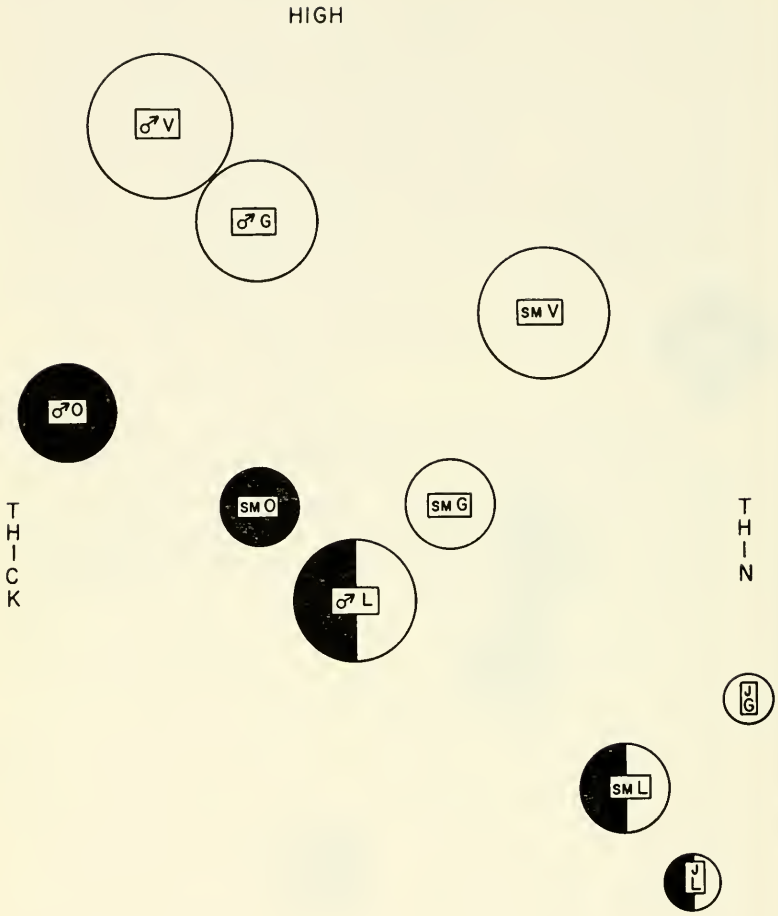

Figure 2. Port Antonio Open. Symbols as in Fig. 1.

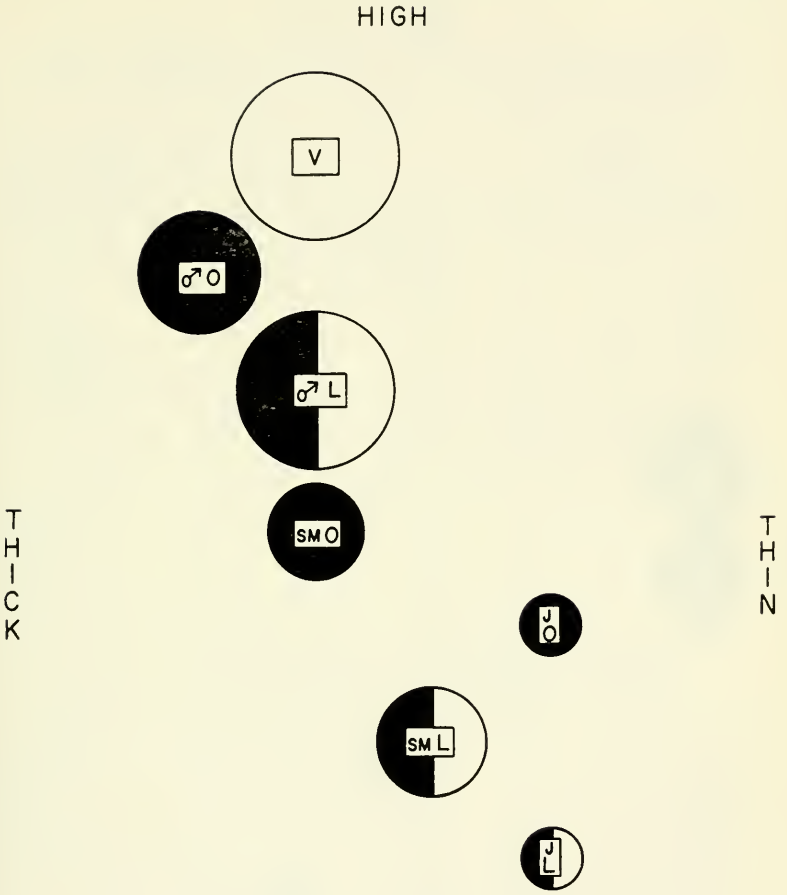

Figure 3. Port Antonio Closed. Symbols as in Fig. 1.

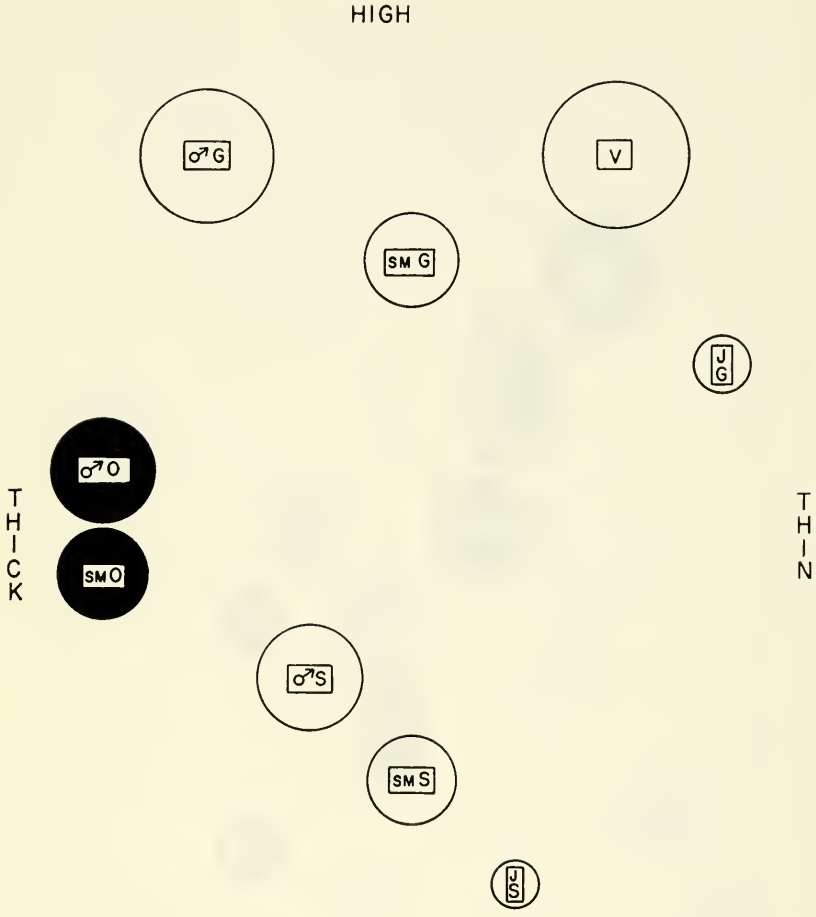

Figure 4. Whitehouse. Symbols as in Fig. 1. S = *sagrei*.

Table 1. Mona.

Percent observations in various structural habitat categories.

H = >20'; G = ground; R = rocks; N = sample size.

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 385	male grahami	H = 2.3	G = 0	R = 0		
10.5-20	3.6	8.1	6.6	3.8	0	22.1
5-10	3.6	13.8	21.4	9.5	0.3	48.9
3-4 3/4	3.6	5.5	4.6	3.5	0	16.2
<3	3.6	2.6	3.3	2.5	0	10.7
Total	12.4	30.0	35.9	19.3	0.3	
N = 246	female-sized grahami	H = 0	G = 0.3	R = 0		
10.5-20	0.7	2.7	2.9	2.6	0	8.9
5-10	0.3	3.4	14.9	28.2	1.0	47.9
3-4 3/4	0.3	2.7	6.0	11.5	0	20.5
<3	2.7	4.1	7.2	8.4	0	22.4
Total	4.1	13.0	30.9	50.6	1.0	
N = 31	juvenile grahami	H = 0	G = 0	R = 3.2		
10.5-20	0	0	0	0	0	0
5-10	0	0	0	25.8	0	25.8
3-4 3/4	0	0	4.8	37.1	3.2	45.1
<3	0	0	6.5	19.4	0	25.9
Total	0	0	11.3	82.3	3.2	
N = 214	male opalinus	H = 0.4	G = 0	R = 0		
10.5-20	1.9	4.2	2.3	1.4	0	9.8
5-10	4.2	21.0	21.3	12.4	0.5	59.4
3-4 3/4	2.3	7.0	6.3	3.5	0	19.1
<3	1.9	5.6	3.3	0.5	0	11.3
Total	10.3	37.8	33.2	17.8	0.5	

Table 1. (cont'd).

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 235	female-sized opalinus		H = 0	G = 0.9	R = 0	
10.5-20	0.4	2.1	1.3	0.9	0	4.7
5-10	2.6	10.2	18.1	14.3	0	45.2
3-4 3/4	1.7	4.7	10.9	7.5	0	24.8
<3	3.4	8.1	8.3	4.9	0	24.7
Total	8.1	25.1	38.6	27.6	0	
N = 15	juvenile opalinus		H = 0	G = 0	R = 0	
10.5-20	0	0	0	0	0	0
5-10	0	0	0	22.2	0	22.2
3-4 3/4	0	0	0	11.1	0	11.1
<3	0	11.1	22.2	33.3	0	66.6
Total	0	11.1	22.2	66.6	0	
N = 838	male lineatopus		H = 0.2	G = 0.8	R = 0	
10.5-20	0.4	1.1	1.8	0.1	0	3.4
5-10	2.6	13.4	22.6	13.0	0	51.6
3-4 3/4	2.1	7.2	14.1	9.5	0.1	33.0
<3	1.7	2.5	3.6	3.0	0	10.8
Total	6.8	24.2	42.1	25.6	0.1	
N = 436	female-sized lineatopus		H = 0	G = 4.4	R = 0	
10.5-20	0	0	0	0	0	0
5-10	0.5	1.4	6.0	3.9	0.2	12.0
3-4 3/4	0.5	4.6	8.4	18.9	0	32.4
<3	1.4	8.3	16.3	24.8	0.7	51.5
Total	2.4	14.3	30.7	47.6	0.9	

Table 1. (cont'd).

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 24	juvenile lineatopus		H = 0	G = 12.5	R = 0	
10.5-20	0	0	0	0	0	0
5-10	0	0	0	0	0	0
3-4 3/4	0	4.2	0	8.8	0	12.5
<3	0	8.3	2.1	56.3	8.3	75.0
Total	0	12.5	2.1	64.6	8.3	
N = 15	male valencienni		H = 6.7	G = 0	R = 0	
10.5-20	0	6.7	6.7	13.3	0	26.7
5-10	0	6.7	6.7	33.3	0	46.7
3-4 3/4	0	0	0	13.3	0	13.3
<3	0	0	0	6.7	0	6.7
Total	0	13.4	13.4	66.6	0	
N = 16	female-sized valencienni		H = 6.3	G = 0	R = 0	
10.5-20	0	6.3	6.3	12.5	0	25.1
5-10	0	12.5	6.3	6.3	0	25.1
3-4 3/4	6.3	6.3	0	12.5	0	25.1
<3	0	0	0	18.8	0	18.8
Total	6.3	25.1	12.6	50.1	0	
N = 3	juvenile valencienni		H = 0	G = 0	R = 0	
10.5-20	0	0	0	33.3	0	33.3
5-10	0	0	0	0	0	0
3-4 3/4	0	0	0	0	0	0
<3	0	0	0	66.7	0	66.7
Total	0	0	0	100.0	0	

Table 2. Port Antonio Open.

Percent observations in various structural habitat categories.

H = >20'; G = ground; R = rocks; N = sample size.

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 146	male grahami	H = 4.1	G = 1.4	R = 0		
10.5-20	2.7	6.9	2.7	0	0	12.3
5-10	5.5	7.5	12.3	11.0	0	36.3
3-4 3/4	5.5	3.4	1.7	9.9	0.7	21.2
<3	4.8	2.1	6.8	8.9	2.1	24.6
Total	18.5	19.9	23.6	29.8	2.7	
N = 163	female-sized grahami	H = 0.6	G = 2.5	R = 0		
10.5-20	0.6	0.6	0.6	0	0	1.8
5-10	1.2	2.5	7.7	5.2	0	16.6
3-4 3/4	1.2	0	2.8	10.7	1.8	16.6
<3	3.7	2.5	4.6	34.7	16.6	62.0
Total	6.8	5.5	15.6	50.6	18.4	
N = 75	juvenile grahami	H = 0	G = 0	R = 0		
10.5-20	0	0	0	0	0	0
5-10	0	0	0	0	0	0
3-4 3/4	0	0	0	10.7	0	10.7
<3	0	0	1.3	57.3	30.7	89.4
Total	0	0	1.3	68.0	30.7	
N = 176	male opalinus	H = 1.1	G = 0	R = 0		
10.5-20	0.6	1.7	10.8	1.7	0	14.8
5-10	5.7	15.9	12.8	4.3	0	38.6
3-4 3/4	6.3	11.4	5.4	6.0	0	29.0
<3	4.6	7.4	0.6	3.4	0.6	16.5
Total	17.1	36.4	29.6	15.3	0.6	

Table 2. (cont'd).

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 136	female-sized opalinus H = 0 G = 0 R = 0					
10.5-20	0	1.5	0	0	0	1.5
5-10	3.7	5.2	14.3	4.8	0.7	28.7
3-4 3/4	3.7	2.9	5.5	7.0	0.7	19.9
<3	2.9	6.6	11.0	27.9	1.5	50.0
Total	10.3	16.2	30.9	39.7	3.0	
N = 21	juvenile opalinus H = 0 G = 0 R = 0					
10.5-20	0	0	0	0	0	0
5-10	0	0	4.8	4.8	0	9.5
3-4 3/4	0	0	0	14.3	0	14.3
<3	0	0	9.5	66.7	0	76.2
Total	0	0	14.3	85.7	0	
N = 183	male lineatopus H = 0 G = 3.3 R = 0					
10.5-20	0	0	0	0	0	0
5-10	0	1.1	1.6	3.8	0	6.6
3-4 3/4	2.2	6.6	5.2	13.4	0.6	27.9
<3	3.8	7.7	12.0	37.7	1.1	62.3
Total	6.0	15.3	18.9	54.9	1.6	
N = 110	female-sized lineatopus H = 0 G = 11.8 R = 0					
10.5-20	0	0	0	0	0	0
5-10	0	0	0	0	0	0
3-4 3/4	0	0	0.5	5.0	0.9	6.4
<3	0	0.9	9.1	63.6	8.2	81.8
Total	0	0.9	9.5	68.6	9.1	

Table 2. (cont'd).

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 23	juvenile lineatopus		H = 0	G = 26.1	R = 0	
10.5-20	0	0	0	0	0	0
5-10	0	0	0	0	0	0
3-4 3/4	0	0	0	0	0	0
<3	0	0	0	56.5	17.4	73.9
Total	0	0	0	56.5	17.4	
N = 25	male valencienni		H = 4.0	G = 0	R = 0	
10.5-20	8.0	12.0	16.0	0	0	36.0
5-10	8.0	12.0	12.0	8.0	0	40.0
3-4 3/4	4.0	4.0	0	0	0	8.0
<3	0	0	4.0	8.0	0	12.0
Total	20.0	28.0	32.0	16.0	0	
N = 36	female-sized valencienni		H = 2.8	G = 0	R = 0	
10.5-20	2.8	0	0	0	0	2.8
5-10	2.8	2.8	8.3	19.5	0	33.4
3-4 3/4	2.8	8.3	0	11.1	2.8	25.0
<3	2.8	0	0	33.3	0	36.1
Total	11.1	11.1	8.3	63.9	2.8	
N = 3	juvenile valencienni		H = 0	G = 0	R = 0	
10.5-20	0	0	0	0	0	0
5-10	0	0	0	33.3	0	33.3
3-4 3/4	0	0	0	0	0	0
<3	0	0	0	66.7	0	66.7
Total	0	0	0	100.0	0	

Table 3. Port Antonio Closed.

Percent observations in various structural habitat categories.

H = >20'; G = ground; R = rocks; N = sample size.

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 185	male opalinus		H = 1.6	G = 0.5	R = 0	
10.5-20	6.5	1.6	1.6	2.2	0	11.9
5-10	7.0	9.7	22.2	9.7	0	48.6
3-4 3/4	5.9	1.6	8.6	2.7	1.1	19.9
<3	1.6	2.7	9.2	3.2	0.5	17.2
Total	21.1	15.7	41.6	17.8	1.6	
N = 206	female-sized opalinus		H = 1.0	G = 2.4	R = 0	
10.5-20	0.5	0.5	0.7	1.2	0	2.9
5-10	8.3	3.4	9.5	15.8	0	37.0
3-4 3/4	5.3	1.5	5.8	6.8	0.5	19.9
<3	6.3	3.9	9.5	15.8	1.5	37.0
Total	20.4	9.2	25.5	39.6	1.9	
N = 79	juvenile opalinus		H = 0	G = 0	R = 0	
10.5-20	0	0	0	0	0	0
5-10	0	1.3	1.3	19.0	0	21.5
3-4 3/4	0	0	0	17.7	0	17.7
<3	0	0	9.5	50.0	1.3	60.8
Total	0	1.3	10.8	86.7	1.3	
N = 122	male lineatopus		H = 0	G = 0	R = 0	
10.5-20	0	0	0	0	0	0
5-10	4.1	3.3	15.6	14.8	0	37.7
3-4 3/4	5.7	3.3	10.2	18.4	0.8	38.5
<3	4.1	3.3	9.0	7.4	0	23.8
Total	13.9	9.9	34.8	40.6	0.8	

Table 3. (concl'd).

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 112	female-sized lineatopus		H = 0	G = 3.6		R = 0
10.5-20	0	0	0	0	0	0
5-10	0	0.9	0.9	8.9	0	10.7
3-4 3/4	0	0.9	4.9	21.0	0.9	27.7
<3	2.7	1.8	16.5	30.8	6.3	58.0
Total	2.7	3.6	22.3	60.7	7.2	
N = 32	juvenile lineatopus		H = 0	G = 3.1		R = 0
10.5-20	0	0	0	0	0	0
5-10	0	0	0	6.3	0	6.3
3-4 3/4	0	0	0	6.3	0	6.3
<3	0	3.1	9.4	53.1	18.8	84.4
Total	0	3.1	9.4	65.7	18.8	
N = 13	valencienni		H = 0	G = 0		R = 0
10.5-20	7.7	7.7	15.4	7.7	0	38.5
5-10	0	0	15.4	15.4	0	30.8
3-4 3/4	15.4	7.7	0	7.7	0	30.8
<3	0	0	0	0	0	0
Total	23.1	15.4	30.8	30.8	0	

Table 4. Whitehouse.

Percent observations in various structural habitat categories.

H = 20'; G = ground; R = rocks; N = sample size.

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 219	male grahami	H = 1.4	G = 0.5	R = 0		
10.5-20	1.8	1.8	2.3	1.4	0	7.3
5-10	2.7	9.6	21.5	9.1	2.3	45.2
3-4 3/4	0.5	7.3	10.1	4.1	0.5	22.5
<3	1.8	10.1	7.1	4.3	0	28.3
Total	6.8	28.8	41.0	18.9	2.8	
N = 284	female-sized grahami	H = 0	G = 2.5	R = 0.4		
10.5-20	0	0	0.4	0.7	0	1.1
5-10	0.7	2.8	14.1	21.8	4.6	44.0
3-4 3/4	1.8	1.8	5.8	7.9	2.5	19.8
<3	1.4	9.9	12.3	7.7	1.1	32.4
Total	2.9	14.5	32.6	38.1	8.2	
N = 54	juvenile grahami	H = 0	G = 0	R = 0		
10.5-20	0	0	0	0	0	0
5-10	0	0	3.7	38.9	0	42.6
3-4 3/4	0	1.9	1.9	31.5	0	35.3
<3	0	0	6.5	13.9	1.9	22.3
Total	0	1.9	12.1	84.3	1.9	
N = 88	male opalinus	H = 0	G = 0	R = 0		
10.5-20	0	0	0	0	0	0
5-10	1.1	6.8	18.2	4.6	0	30.7
3-4 3/4	2.3	13.6	15.9	1.1	0	32.9
<3	1.1	20.5	9.1	4.6	1.1	36.4
Total	4.5	40.9	43.2	10.3	1.1	

Table 4. (cont'd).

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 72	female-sized opalinus		H = 0	G = 2.8		R = 0
10.5-20	0	0	0	0	0	0
5-10	0	5.6	7.0	1.4	0	14.0
3-4 3/4	2.8	4.2	16.7	1.4	0	25.1
<3	2.8	31.9	19.5	4.2	0	58.4
Total	5.6	41.7	43.2	7.0	0	
N = 10	juvenile opalinus		H = 0	G = 0	R = 0	
10.5-20	0	0	0	0	0	0
5-10	0	0	10.0	20.0	0	30.0
3-4 3/4	0	10.0	10.0	20.0	0	40.0
<3	0	10.0	10.0	10.0	0	30.0
Total	0	20.0	30.0	50.0	0	
N = 263	male sagrei		H = 0	G = 6.5	R = 2.7	
10.5-20	0	0	0	0	0	0
5-10	0	0.8	1.5	0	0	2.3
3-4 3/4	0	6.5	8.4	2.3	0	17.2
<3	2.3	30.0	27.8	11.4	0	71.5
Total	2.3	37.3	37.7	13.7	0	
N = 393	female-sized sagrei		H = 0	G = 13.2		R = 4.8
10.5-20	0	0	0	0	0	0
5-10	0	0	0.8	0.3	0	1.1
3-4 3/4	0	1.6	1.3	0.3	0	3.2
<3	2.5	31.8	22.5	21.0	0	77.8
Total	2.5	33.4	24.6	21.6	0	

Table 4. (concl'd).

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 251	juvenile sagrei		H = 0	G = 31.9	R = 4.0	
10.5-20	0	0	0	0	0	0
5-10	0	0	0.8	1.6	0	2.4
3-4 3/4	0	0.8	0.4	2.0	0	3.2
<3	2.0	17.8	12.6	25.6	0.4	58.4
Total	2.0	18.6	13.8	29.2	0.4	
N = 7	male valencienni		H = 0	G = 0	R = 0	
10.5-20	0	0	0	0	0	0
5-10	14.3	0	28.6	42.9	0	85.8
3-4 3/4	0	0	14.3	0	0	14.3
<3	0	0	0	0	0	0
Total	14.3	0	42.9	42.9	0	
N = 8	female-sized valencienni		H = 0	G = 0	R = 0	
10.5-20	0	0	0	0	0	0
5-10	0	0	0	25.0	0	25.0
3-4 3/4	0	0	37.5	0	0	37.5
<3	0	0	0	37.5	0	37.5
Total	0	0	37.5	62.5	0	
N = 7	juvenile valencienni		H = 0	G = 0	R = 0	
10.5-20	0	0	0	0	0	0
5-10	0	0	42.9	14.3	0	57.2
3-4 3/4	0	0	0	28.6	0	28.6
<3	0	0	14.3	0	0	14.3
Total	0	0	57.2	42.9	0	

Table 5. Percent observations for Whitehouse species in climatic categories.

	Sun	Shade	Clouds
male *sagrei*	17.4	74.4	8.3
female-sized *sagrei*	15.9	73.8	10.2
juvenile *sagrei*	33.8	58.8	7.4
male *grahami*	12.4	74.6	12.9
female-sized *grahami*	20.5	61.4	18.1
juvenile *grahami*	15.7	66.7	17.6
male *opalinus*	3.5	72.1	24.4
small *opalinus*	14.5	66.3	19.3
valencienni	36.4	50.0	13.6

Table 6. Statistical significance for Mona comparisons [a]

group vs. height / group vs. diameter	grahami ♂	female-sized grahami	grahami juvenile	lineatopus ♂	female-sized lineatopus	lineatopus juvenile	opalinus ♂	small opalinus	valencienni ♂	female-sized valencienni
grahami ♂		1	1	1	1	1	1	1	1*	0
female-sized grahami	1*		1	1	1	1	1*	1*	1*	1*
grahami juvenile	1*	1*		1*	1	1	1*	1	1*	1*
lineatopus ♂	1*	1	1		1	1	1*	1	1*	1*
female-sized lineatopus	1*	0	1	1*		1	1*	1*	1*	1*
lineatopus juvenile	1*	1*	0	1*	1*		1*	1*	1*	1*
opalinus ♂	0	1	1	1	1	1		1	1*	1*
small opalinus	1*	1	1	0	1	1	1*		1*	1*
valencienni ♂	1*	0	1	1*	0	0	1*	1*		1
female-sized valencienni	1*	0	1	1*	0	0	1*	1*	0	

Table 6 (concl'd)

comments / height vs. diameter	grahami ♂	female-sized grahami	grahami juvenile	lineatopus ♂	female-sized lineatopus	lineatopus juvenile	opalinus ♂	small opalinus	valencienni ♂	female-sized valencienni
grahami ♂			Z							
female-sized grahami	1(A)		Z							
grahami juvenile	0	0		Z	Z	Z	Z	Z	Z	NS Z
lineatopus ♂	0	1(A)	0					NS		
female-sized lineatopus	0	0	0	1(B)						NS
lineatopus juvenile	0	0	0	0	0					
opalinus ♂	0	1(B)	0	0	1(B)	1(B)				
small opalinus	0	0	0	1(A)	0	0	0			
valencienni ♂	1(A)	1(B)	0	1(B)	0	1(B)	0	0		
female-sized valencienni	1(A)	1(B)	1(B)	1(B)	0	1(B)	0	0	0	

[a] NS = model never significant at 5% level; Z = has zero margins; * = species at top has larger value; A = small diameters at low perches; B = small diameters at high perches; for interpretation of numbers, see "Statistical appendix."

Table 7. Statistical significance for Port Antonio Open comparisons [a]

group vs. height / group vs. diameter	grahami ♂	female-sized grahami	grahami juvenile	lineatopus ♂	female-sized lineatopus	lineatopus juvenile	opalinus ♂	small opalinus	valencienni ♂	small valencienni
grahami ♂		1	1	1	1	1	1	1	1*	1
female-sized grahami	1*		1	1	1	1	1*	0	1*	1*
grahami juvenile	1*	1*		1*	1	1	1*	0	1*	1*
lineatopus ♂	1*	1	1		1	1	1*	1*	1*	1*
female-sized lineatopus	1*	1*	1	1*		1	1*	1*	1*	1*
lineatopus juvenile	1*	1*	0	1*	1*		1*	1*	1*	1*
opalinus ♂	1	1	1	1	1	1		1	1*	0
small opalinus	0	1	1	0	1	1	1*		1*	1*
valencienni ♂	0	0	1	1	1	1	0	1		0
small valencienni	1*	1*	1	1*	1	1	1*	1*	1*	

Table 7 (concl'd)

comments / height vs. diameter	grahami ♂	female-sized grahami	grahami juvenile	lineatopus ♂	female-sized lineatopus	lineatopus juvenile	opalinus ♂	small opalinus	valencienni ♂	small valencienni
grahami ♂										
female-sized grahami	1(A)			NS		Z				
grahami juvenile	0	0							Z	
lineatopus ♂	0	1(A)	1(A)					NS	NS	
female-sized lineatopus	0	0	0	0			NS		Z	
lineatopus juvenile	0	0	0	0	0		Z		Z	Z
opalinus ♂	1(A)	1(A)	0	1(A)	1(A)	1(A)				
small opalinus	1(A)	1(A)	1(A)	1(A)	1(A)	0	1(A)			
valencienni ♂	1(A)	1(A)	0	0	0	0	0	0		
small valencienni	1(A)	1(A)	0	1(A)	0	0	1(A)	1(A)	1(A)	

[a] NS = model never significant at 5% level; Z = has zero margins; * = species at top has larger value; A = small diameters at low perches; for interpretation of numbers, see "Statistical appendix."

Table 8. Statistical significance for Port Antonio Closed comparisons [a]

group vs. height / group vs. diameter	opalinus ♂	female-sized opalinus	opalinus juvenile	lineatopus ♂	female-sized lineatopus	lineatopus juvenile	valencienni
opalinus ♂		1	1	1	1	1	1*
female-sized opalinus	1*		1	1*	1	1	1*
opalinus juvenile	1*	1*		1*	1	1	1*
lineatopus ♂	1*	0	1		1	1	1*
female-sized lineatopus	1*	1*	1	1*		1	1*
lineatopus juvenile	1*	1*	0	1*	1*		1*
valencienni	1*	0	1	0	1	1	

Table 8. (concl'd).

group vs. diameter \ comments	opalinus ♂	female-sized opalinus	opalinus juvenile	lineatopus ♂	female-sized lineatopus	lineatopus juvenile	valencienni
opalinus ♂							
female-sized opalinus	0						Z
opalinus juvenile	0	0					
lineatopus ♂	0	0	0				
female-sized lineatopus	0	0	0	1(B)			
lineatopus juvenile	0	0	0	0	0		Z
valencienni	0	0	0	0	0	0	

[a] Z = has zero margins; * = species at top has larger value; B = small diameters at high perches; for interpretation of numbers, see "Statistical appendix."

Table 9. Statistical significance for Whitehouse comparisons [a]

group vs. height / group vs. diameter	sagrei ♂	female-sized sagrei	sagrei juvenile	grahami ♂	female-sized grahami	grahami juvenile	opalinus ♂	small opalinus	valencienni
sagrei ♂		1+	1	1*	1*+	1*	1*	1*	1*+
female-sized sagrei	1*		1	1*	1*+	1*	1*	1*	1*+
sagrei juvenile	1*	1*		1*	1*	1*	1*	1*	1*+
grahami ♂	1	1	1		1	1	1	1	0
female-sized grahami	1*	0	0	1*		0	1*	1	0
grahami juvenile	1*	1*	1*	1*	1*		2	0	0
opalinus ♂	0	1	1	0	1	1		1	2*
small opalinus	0	1	1	0	1	1	0		1*
valencienni	1*	1*	2*	1*	1*	1	1*	1*	

group vs. insolation / height vs. diameter	sagrei ♂	female-sized sagrei	sagrei juvenile	grahami ♂	female-sized grahami	grahami juvenile	opalinus ♂	small opalinus	valencienni
sagrei ♂		0	0	0	1*(E)	0	1*(C)	0	0
female-sized sagrei	0		1(C)	0	2*(E)	0	1(D)	0	0
sagrei juvenile	1(A)	0		2*(C)	1*(C)	2*(C)	1*(C)	0	0
grahami ♂	0	0	0		1*(E)	0	1*(C)	0	2*(E)
female-sized grahami	1(B)	1(B)	1(A)	1(B)		0	1*(C)	0	0
grahami juvenile	0	0	0	0	1(B)		0	0	0
opalinus ♂	0	0	0	0	1(B)	0		1(C)	1(C)
small opalinus	0	0	3(A)	0	1(B)	1(B)	0		0
valencienni	0	0	0	0	1(B)	1(B)	0	0	

Table 9 (concl'd)

height vs. insolation / diameter vs. insolation	sagrei ♂	female-sized sagrei	sagrei juvenile	grahami ♂	female-sized grahami	grahami juvenile	opalinus ♂	small opalinus	valencienni
sagrei ♂		1(H)	1(H)	0	0	2(I)	0	0	0
female-sized sagrei	1(M)		1(H)	3(G)	0	0	0	0	0
sagrei juvenile	1(J)	1(M)		0	0	0	0	0	0
grahami ♂	0	0	1(J)		0	0	0	0	0
female-sized grahami	1(M)	1(M)	1(M)	1(J)		0	0	0	0
grahami juvenile	1(M)	0	1(M)	3(J)	1(L)		0	0	0
opalinus ♂	1(J)	1(M)	1(J)	0	0	2(J)		0	0
small opalinus	0	0	1(J)	0	0	3(J)	0		0
valencienni	1(J)	0	1(J)	0	0	0	0	0	

[a] * = species at top has larger value; + = model never significant at 5% level, 3-way interactions fitted; A = small diameters at low perches; B = small diameters at high perches; C = more in shade and clouds; D = more in shade and sun: E = more in sun and clouds; F = highest in sun and lowest in shade; G = highest in clouds and lowest in shade; H = highest in shade and lowest in sun; I = highest in clouds and lowest in sun; J = thinnest in sun and thickest in clouds; K = thickest in sun and thinnest in shade; L = thinnest in shade and thickest in clouds; M = thinnest in sun and thickest in shade; for interpretation of numbers, see "Statistical appendix."

Table 10. Points at which data were broken for perch height and diameter.

Mona

diameter (inches) \ height (feet)	grahami ♂	female-sized grahami	grahami juvenile	lineatopus ♂	female-sized lineatopus	lineatopus juvenile	opalinus ♂	small opalinus	valencienni ♂	female-sized valencienni
grahami ♂		7 1/4	5 3/4	6 3/4	4 1/4	3	7 1/4	7	6	5
female-sized grahami	7/8		5 1/4	6	4 1/4	3	3	6 3/4	7 3/4	7 3/4
grahami juvenile	1	1		4 3/4	2 1/4	2 1/4	4 1/4	5 1/4	6	7
lineatopus ♂	3	7/8	1		4 3/4	3	6	2 1/2	6	7 3/4
female-sized lineatopus	1 1/4	3/8	1	7/8		2 1/4	4	4 1/4	6	6 1/4
lineatopus juvenile	5/8	5/8	1	5/8	5/8		3	3	3	3
opalinus ♂	1 3/4	1 3/4	1	1 3/4	1 3/4	7/8		3 1/4	7 3/4	10
small opalinus	2	1	1	1 1/2	1	5/8	1 3/4		7 3/4	7 3/4
valencienni ♂	3/4	3/4	1/4	3/4	3/4	5/8	3/4	3/4		5
female-sized valencienni	3/4	2 1/4	1	3/4	2 1/4	5/8	3/4	3/4	1 1/2	

Port Antonio Closed

height (feet) / diameter (inches)	opalinus ♂	female-sized opalinus	opalinus juvenile	lineatopus ♂	female-sized lineatopus	lineatopus juvenile	valencienni
opalinus ♂		3 3/4	3 1/2	6 3/4	4 1/4	2	10
female-sized opalinus	1		3 1/2	2 1/4	4 1/4	2	2 3/4
opalinus juvenile	7/8	3/4		2 1/4	6 1/4	1	3 1/2
lineatopus ♂	1	2 3/4	3/4		3	2	8
female-sized lineatopus	1	3/4	3/4	5/8		2	3
lineatopus juvenile	5/8	5/8	5/8	5/8	5/8		2
valencienni	3/8	1 3/4	7/8	3	1 3/4	5/8	

Port Antonio Open

diameter (inches) \ height (feet)	grahami ♂	female-sized grahami	grahami juvenile	lineatopus ♂	female-sized lineatopus	lineatopus juvenile	opalinus ♂	small opalinus	valencienni ♂	small valencienni
grahami ♂		3 1/2	2 1/4	3 1/2	2 1/4	1 1/4	10	2	6 3/4	3
female-sized grahami	3/4		1 1/2	5	1 3/4	1 1/4	3 1/4	3 3/4	5 3/4	5 3/4
grahami juvenile	3/8	3/8		1 1/2	1	1	3	3 1/2	2 1/4	1 1/2
lineatopus ♂	3/4	3/8	3/8		1 3/4	1 1/4	3	3 1/2	5	5
female-sized lineatopus	5/8	3/8	1/4	3/8		1 1/4	2	1 3/4	2 1/4	1 1/2
lineatopus juvenile	5/8	3/8	1/4	3/8	1/4		1 1/4	1 1/4	1 1/4	1 1/4
opalinus ♂	1 1/2	7/8	3/8	1	1	5/8		2	6 3/4	3
small opalinus	2	7/8	3/8	7/8	5/8	3/8	2		6 3/4	1 1/2
valencienni ♂	1 1/4	7/8	5/8	7/8	7/8	5/8	4	2 1/4		6 3/4
small valencienni	3/4	3/8	3/8	3/8	1 1/2	5/8	3/4	3/4	3/4	

Table 10 (concl'd)

Whitehouse

diameter (inches) \ height (feet)	sagrei ♂	female-sized sagrei	sagrei juvenile	grahami ♂	female-sized grahami	grahami juvenile	opalinus ♂	small opalinus	valencienni
sagrei ♂		1 1/6	1 1/6	3 1/2	3 1/2	3 1/4	3 1/2	3 1/4	3 1/2
female-sized sagrei	3/4		11/12	2 1/2	2 1/2	2 3/4	2	2	2 3/4
sagrei juvenile	7/8	7/8		1 3/4	1 1/6	2	1 3/4	1 1/6	2
grahami ♂	4	4	7/8		4 1/4	7	4 1/4	4	7 3/4
female-sized grahami	1 3/4	1 3/4	2	3/4		3 1/4	5 1/4	4	3 1/4
grahami juvenile	7/8	7/8	7/8	7/8	7/8		3 1/4	3 1/2	5 3/4
opalinus ♂	1 1/4	1 1/4	7/8	1 1/4	1 1/2	7/8		3 3/4	3 1/4
small opalinus	2 3/4	3/4	7/8	2 3/4	2	7/8	1 1/4		3 3/4
valencienni	1 1/4	1 1/4	1 1/2	1 1/4	1 1/4	7/8	1 1/4	1	

BREVIORA

Museum of Comparative Zoology

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LITHOPHAGA ARISTATA IN THE SHELL-PLATES OF CHITONS (MOLLUSCA)

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and
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ABSTRACT. The occurrence of the mytilid bivalve *Lithophaga aristata* as a borer into the shell-plates of polyplacophorans is unreported. Our investigation revealed this lithophage in the Panamic *Chiton stokesii* and, less commonly, in the West Indian *C. tuberculatus*. A review of other organisms known to associate with chitons is provided, although none is apparently deleterious to the host-species as in the case of *Lithophaga*. Damage to the chiton by *L. aristata* appears to consist predominantly of the weakening of the shell-plates and not the destruction of the aesthetes of the nervous system.

INTRODUCTION

Although several symbiotic organisms are known to live in association with chitons, the boring of the mytilid bivalve *Lithophaga* into the shell-plates of polyplacophorans appears to be unreported in the literature. During a dissection of a specimen of *Chiton stokesii* Broderip, 1832, several *Lithophaga* (*Myoforceps*) *aristata* (Dillwyn, 1817) were discovered in the shell-plates. A survey was undertaken to assess the occurrence, and to determine the nature, of the infestation of *Lithophaga* in *C. stokesii* and other species of chitons from various localities. In addition, the known symbionts of chitons were reviewed. The results, presented in this paper, indicate that the presence of *Lithophaga* in the shell-plates of chitons is unusual and represents the most detrimental polyplacophoran symbiont known. We have observed *L. aristata* boring in the shell-plates of the Panamic *Chiton stokesii* and the Caribbean *Chiton tuberculatus* Linnaeus, 1758.

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METHODS AND MATERIALS

Numerous specimens of *Chiton stokesii,* collected at various localities in the Gulf of Panama by the senior author during July and August 1969, were examined by radiographic techniques for the presence of *Lithophaga.* A survey was made of the large collection of Polyplacophora in the Museum of Comparative Zoology, Harvard University, in an effort to locate other species hosting *Lithophaga,* and X-rays of suspected host-individuals were made. All radiographs were checked for the number of lithophages present, their spatial distribution, and orientation. Borers were extracted at random to check their identity and all proved to be *L. aristata.*

POLYPLACOPHORAN SYMBIONTS

Few records are to be found in the literature concerning symbionts of polyplacophorans, but organisms representing several phyla are associated with chitons. *Cryptochiton stelleri* (Middendorff, 1846) is known to harbor two commensals: a crustacean, *Opisthopus transversus* (Rathbun, 1893) and an annelid, *Arctonoe vittata* (Grube, 1855) (MacGinitie and MacGinitie, 1968; Webster, 1968).

Glynn (1968) and Menzies and Glynn (1968) summarized present knowledge of the symbionts of the mantle cavity on the West Indian chitonids, *Acanthopleura granulata* (Gmelin, 1791) and *Chiton tuberculatus* Linnaeus, 1758. Included were: the isopods, *Dynamenella perforata* (Moore, 1901) with *A. granulata* and *C. tuberculatus; Exosphaeroma alba* Menzies and Glynn,

1968, *Exosphaeroma crenulatum* (Richardson, 1902), *Dynamenopsis dianae* Menzies, 1962 with *C. tuberculatus; Exosphaeroma alba* var. *chromata* Menzies and Glynn, 1968 with *C. marmoratus* Gmelin, 1791; and the foraminiferan, *Acervulina inhaerens* Schulze, 1854 and the amphipod, *Parhyale hawaiensis* (Dana, 1853) both with *C. tuberculatus;* the harpacticoids, *Harpacticus* sp. and *Heterolaophonte* sp. with *A. granulata* and *C. tuberculatus;* and the collembolan, *Actaletes neptuni* Giard, 1889 with *A. granulata.*

The mite *Halixodes chitonis* (Brucker, 1897) has been found attached to the gills of the Neozelanic *Cryptoconchus porosus* (Burrow, 1815) (Brucker, 1897; Brucker and Trouessart, 1900). Helfman (1968) observed the ctenostomatous ectoproct *Farella elongata* (van Beneden, 1845) in the ventral girdle tissue bordering the pallial groove. Arey and Crozier (1919) reported the following symbionts on the shell-plates of *C. tuberculatus:* the barnacle, *Tetraclita;* the polychaetes, *Spirorbis* and *Serpula;* and algae, including the *"Enteromorphas."* They mentioned that the algae afforded protection for various young mollusks, nematodes, archiannelids, and protozoans. None of these symbionts has been shown to be harmful to the host.

After conducting extensive studies on *Chiton tuberculatus,* Arey and Crozier (1919: 171–172) remarked: "The general impression derived from the consideration of destructive agents in relation to *Chiton* is that these mollusks are very efficiently protected. The length of life which they seem to attain, the variety of habitats which they frequent, and the character of their sensory responses, which determine certain features of their life in their habitats, afford important evidence to this effect."

While the above statement is generally true for *C. tuberculatus,* the Panamic *C. stokesii* appears far more vulnerable to attack by destructive agents than *C. tuberculatus.* We observed large individuals of *C. stokesii* from different localities that were not only greatly eroded, but heavily fouled with calcareous algae, bryozoans, and polychaete tubes. Most of the latter were heavily infested with *Lithophaga aristata,* some of which had grown large enough to fall out of their burrows, leaving greatly weakened shell-plates. The cases of *C. tuberculatus* from Trinidad (MCZ 31955) and Isla Margarita (MCZ 273763), in which we found examples harboring *L. aristata,* appear to be rare. Our examination of numerous other

samples of *C. tuberculatus* produced no additional *Lithophaga*. It is probable that differences in shell-structure account for the greater penetrability and susceptibility for fouling and boring in *C. stokesii*.

RESULTS AND DISCUSSION

The mytilid bivalve *Lithophaga* (*Myoforceps*) *aristata* (Dillwyn, 1817) (Figs. 7 and 8) bores into calcareous substrates, including the shells of large bivalves (e.g., *Spondylus, Chama, Ostrea*) and gastropods (e.g., *Haliotis, Patella, Strombus,* and *Pleuroploca*). The species occurs in warm temperate to tropical waters in the eastern Pacific, western Atlantic, and eastern Atlantic regions and is usually found in shallow water, although Soot-Ryen (1955) reported a living specimen taken from 165 fathoms (Turner and Boss, 1962).

In both *C. stokesii* and *C. tuberculatus, Lithophaga aristata* was present only in large specimens. This relationship coincides with the findings of Arey and Crozier (1919) and Crozier and Arey (1920) who observed the presence of barnacles, polychaetes, and algae only on larger *C. tuberculatus*. The erosion of the shell-plates, which is brought about by physical agents of the environment and by organisms which live on the chiton's shell, appears to be a prerequisite for the boring of *Lithophaga*. During settlement the pediveligers of *L. aristata* evidently reject the uneroded areas of the polyplacophoran shell and metamorphosis occurs on the eroded substrate. We noted that most lithophages began boring at the posterior edge of the intermediate valves, which was normally eroded in large individuals. Large *C. stokesii* showing little or no erosion had few, if any, *L. aristata;* the valves of those chitons that were considerably eroded revealed *Lithophaga* boring in them at various places, not just at the posterior edge. *Chiton viridis* Spengler, 1797, a Caribbean species that normally lives below the low-water mark, is rarely eroded and no *Lithophaga* were found in the shell-plates of this species.

After initial penetration of the shell, most *L. aristata* bored horizontally. In several instances we observed the burrows of *Lithophaga* extending into a second valve. In one example from Culebra Island, Canal Zone, which harbored over 40 *L. aristata* (Fig. 1),

two individual lithophages had bored vertically from one valve to the next, penetrating the intervening musculature (Fig. 4). One such burrow passed from valve III into the insertion plate of valve IV (Fig. 1). All cases of vertical burrows apparently occurred in overcrowded conditions.

Most burrows of intermediate valves were roughly parallel with the antero-posterior axis of the chiton with the siphons of the *Lithophaga* pointed posteriorly, although they deviated somewhat by orienting themselves along an axis extending from the zone of erosion toward the nearest growth zone. The reason for this is obvious. Should a lithophage burrow perpendicularly to the antero-posterior axis and only in the region of the mucro, it would risk having its surrounding substrate eroded away. By burrowing from the zone of erosion toward a growth zone, the lithophage is assured of an increasing substrate in which to bore. This explanation clarifies the otherwise haphazard orientation of the burrows in the posterior valve, where the oldest shell material is near the center, not at the posterior edge (Fig. 2).

As the lithophage increases in size, it faces problems caused by the restricted space in which it can grow. Although some *Lithophaga* enlarge their burrows dorsally, most penetrate ventrally and eventually reach the mantle of the chiton. When the latter situation occurs, the chiton secretes a thin calcareous shield in an effort to contain the intrusion of the lithophage. Sometimes more than half of the ventral portion of the lithophage is situated below the ventral shell-plate surface. In spite of the efforts of the *Lithophaga* to increase in size and the chiton's effort to contain it, the lithophage soon reaches a point where further growth is impossible. Whether this represents a truly stenomorphic condition or not is uncertain, because we do not know if the *L. aristata* we observed ever reached sexual maturity. *Lithophaga aristata* is known to attain a length of 52 mm (Turner and Boss, 1962); the largest specimen extracted from a *C. stokesii* was 9.0 mm, while the average length was about 7.0 mm.

There is evidence that at least a few *L. aristata* outgrow their restricted polyplacophoran substrate (Fig. 6). Some of the largest burrows that we examined were exposed along their entire dorsal surface, indicating that the lithophages may have fallen from their

burrows. It is probable that specimens that outgrow the chiton perish in the external environment.[1]

The effect of numerous *Lithophaga* in the shell-plates must be detrimental to Polyplacophora. In addition to damaging the specialized portion of the nervous system that makes up the aesthetes in the tegmentum, *Lithophaga* weakens the valves and, at times, probably affects the maneuverability of the chiton. The seriousness of damage to a large amount of the tegmental nervous tissue is open to question and may depend upon the species involved. Aesthetes are photosensitive, being activated both by light of constant intensity and by a decrease of light intensity (Arey and Crozier, 1919). Studies on the growth and behaviour of *Chiton tuberculatus* indicated that normal erosion of shell-plates and concomitant loss of tegmental aesthete photosensitivity produced at least a partial inversion in its phototropic response. While young *C. tuberculatus* are photonegative, older individuals may be irresponsive or photopositive (Arey and Crozier, 1919; Crozier and Arey, 1920), although Glynn (personal communication) found older *C. tuberculatus* from Puerto Rico also to be photonegative. It appears, then, that *Lithophaga* mainly affects the durability of the shell, rendering the chiton more susceptible to predation.

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[1] Although Hodgkin (1962) maintained *L. plumula kelseyi* Hertlein and Strong, 1946 outside their burrows for over one year under laboratory conditions, Otter (1937) was unsuccessful in his attempts to rear *L. cumingiana* (Reeve, 1857) and *L. teres* (Philippi, 1846) that had been removed from their burrows. It is doubtful if *Lithophaga* could survive out of its burrow under exposed conditions.

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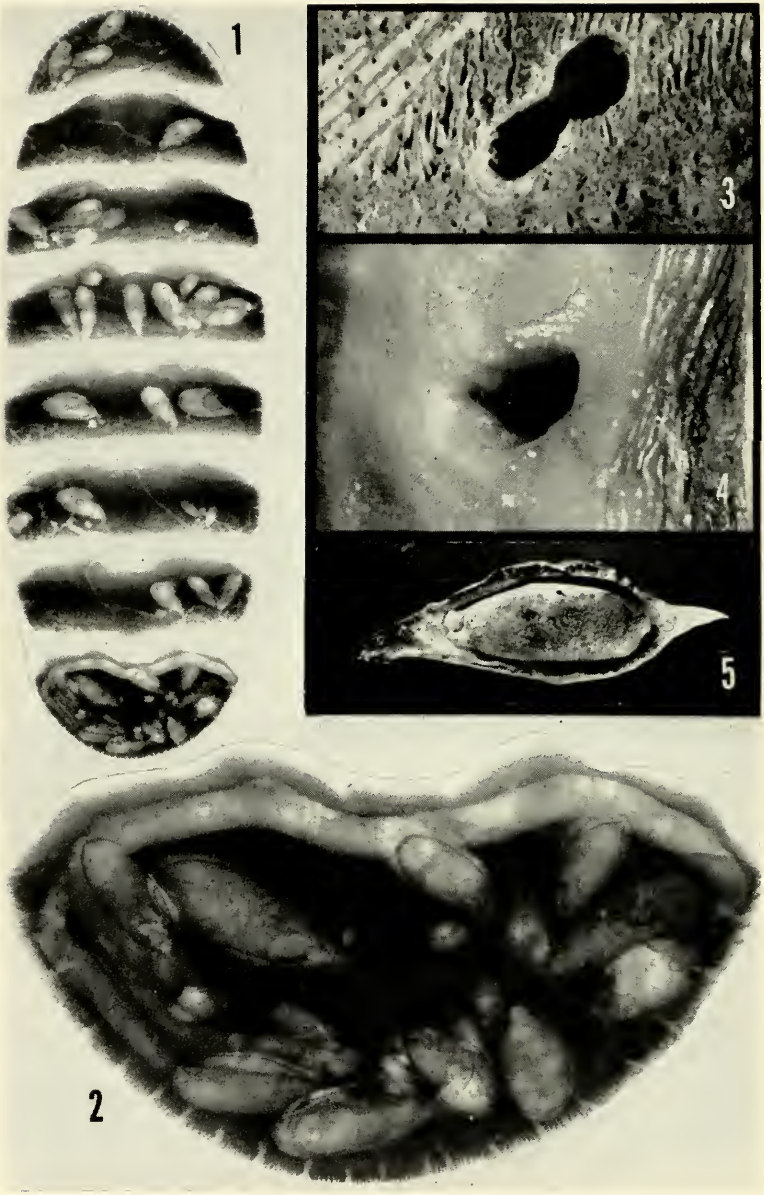
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Figure 1. Radiograph of disarticulated shell-plates from a specimen of *Chiton stokesii* from Culebra Island, Panama Bay, Canal Zone (MCZ 277122), showing a high degree of infestation by *Lithophaga aristata* (0.84 ×).

Figure 2. Enlargement of posterior valve of Fig. 1 (3.2 ×).

Figure 3. Typical siphonal opening of *L. aristata* burrow in an uneroded portion of a *C. stokesii* shell-plate (12 ×).

Figure 4. Intervening shell-plate musculature located between valves IV and V in Fig. 1, showing damage resulting from penetration of *Lithophaga* (9.2 ×).

Figure 5. Example of *L. aristata* (MCZ 277123) in shell-plate cross section of *C. stokesii* from Punta Mala, Panama (3.9 ×).

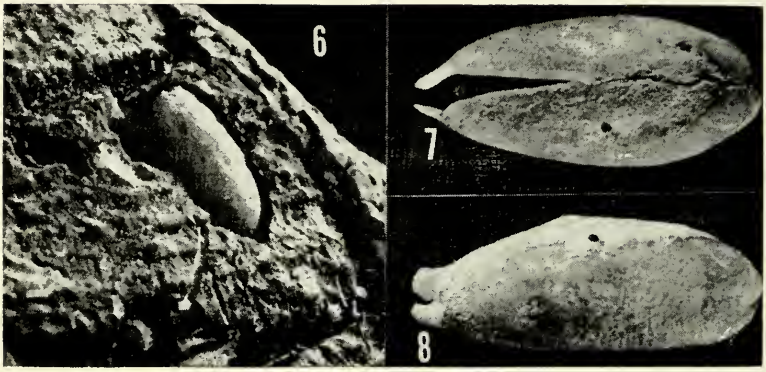

Figure 6. Exposed burrow of *Lithophaga aristata* in *Chiton stokesii* from Panama City, Panama (MCZ 78821) (4.2 ×).

Figures 7–8. *L. aristata* extracted from burrow illustrated in Fig. 5 (MCZ 277123) (6.5 ×).

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ECOLOGICAL OBSERVATIONS ON A LITTLE KNOWN SOUTH AMERICAN ANOLE: *TROPIDODACTYLUS ONCA*

James P. Collins[1]

ABSTRACT. The little known anole *Tropidodactylus onca* on the island of Margarita is typically restricted to belts of low xerophytic vegetation adjacent to the open sandy area of natural beaches. Most animals are found on the ground or in low bushes and occur up to a height of 30.0 cm. They are poor climbers and will occasionally escape into holes made by ghost crabs.

INTRODUCTION

A brief visit (from July 8 to July 21, 1968) to the Fundacion La Salle on Margarita Island, Venezuela, afforded me an opportunity to collect and observe a little known anole, *Tropidodactylus onca.* Margarita is a continental island approximately twenty-one miles off the district of Sucre on the northern coast of Venezuela. It is approximately two hundred air miles northeast of Caracas.

Tropidodactylus onca is a specialized derivative of *Anolis* but with keeled scales underneath the digits instead of the expanded digital pads with adhesive lamellae so characteristic of the latter primarily arboreal genus. The difference in morphology should be reflected in ecology, but there have been no detailed reports on the habits, habitat, or even color in life of *T. onca.* This paper attempts to remedy this gap in information.

Description and color in life. Tropidodactylus onca is a relatively large anole. The largest of the specimens collected is 75 mm snout-vent length. The tail is round with no dorsal crest and is approximately equal to the snout-vent length of the animal.

The most distinctive specialization of the anoles in general, the dewlap, is extremely well developed in this genus. It has a bright yellow ground color in which individual red scales are embedded.

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The dorsal color of the lizard varies from a very light ashy-gray to a dark gray-brown with a disruptive pattern of black and white longitudinal markings. These vary from barely visible to very prominent. The ventral surface of the lizard is white. The species is not sexually dichromatic and is very difficult to sex externally. The cryptic coloration of the species is perfect. In the field the animals are indistinguishable from their surroundings. In fact, an animal can usually be located only when the collector inadvertently frightens it into movement.

Habits and habitat. Tropidodactylus onca is a beach anole. Its distribution is typically restricted to the belt of low xerophytic vegetation adjacent to the open sandy area of a natural beach. The exact width of this belt and its continuity varies according to the geological and ecological factors of the particular locality. The animal was never observed in the open sandy areas devoid of vegetation, and penetrates only slightly into the more landward areas where the vegetation is higher than 0.75 to 1.00 m.

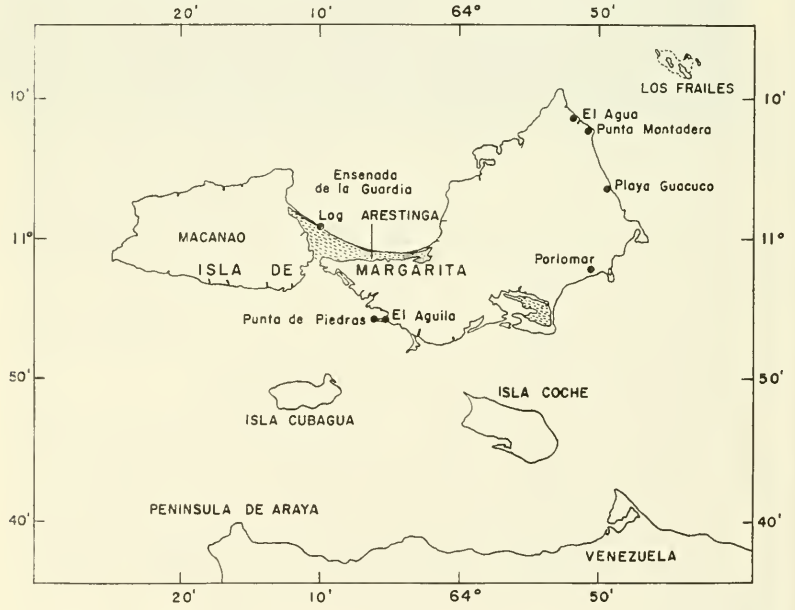

Figure 1. Margarita Island. Localities at which *Tropidodactylus onca* was observed or collected are shown as solid circles.

All the specimens, with the exception of one taken at a height of 1.25 m, were collected on the ground or up to 30.0 cm high on low bushes, vines, etc.

Observation and collecting was restricted to six localities (Fig. 1), all on the eastern half of the island. Roze (1964), however, has reported the lizard from the western half (Macanao). Of the six localities in which the species was observed, five are on the coast. The exception, El Aguila, is a town approximately 2.5 km from Punta de Piedras. Possible reasons for the animal's appearance here will be discussed later. Outside of this single exception, no specimens were ever observed in noncoastal portions of the island and all were collected at sea level.

The vegetation of the zone in which *Tropidodactylus* is found consists of only low ground growth. The sand-shrub communities of the five coastal localities in which *Tropidodactylus* is found each contain at least two and as many as four of the following species of plant: *Sesuvium portulacastrum, Philoxerus vermicularis, Batis maritima, Sporobolus* (*virginicus?*), *Ipomoea* (*pescaprae?*), and *Mallotonia gnaphalodes*. Howard (1950) lists these six species as pan-Caribbean in distribution. These are found in association with less abundant and restricted species, the exact taxa varying from locality to locality. The landward edge of this coastal community typically contains representatives of the genera *Opuntia, Melocactus, Lemairocereus, Philoxocereus,* and *Prosophis*. *Tropidodactylus* penetrates slightly into this zone.

The majority of the animals collected were taken in large patches of *Ipomoea* found at two of the localities investigated (El Agua and Playa Guacuco). The reptile was found both on the plants and in the open space between them. If the patch was dense enough, the animals were typically found with their head on top of the leaves and their trunk and tail among the tangled vines. Some were also found on an occasional outcropping of rock or log. When frightened, the animal would either duck into the mat of vegetation (if dense enough) or scamper across the open sand until it reached a vine or series of vines which it would then proceed to run clumsily over. Being nonwoody, the plants do not give much support and the animal could easily be taken. In the area just north of Punta Montadero where *Mallotonia,* a woody-stem plant, is dominant, the animal's behavior was very different. Here, when first sighted, the lizard was always on the

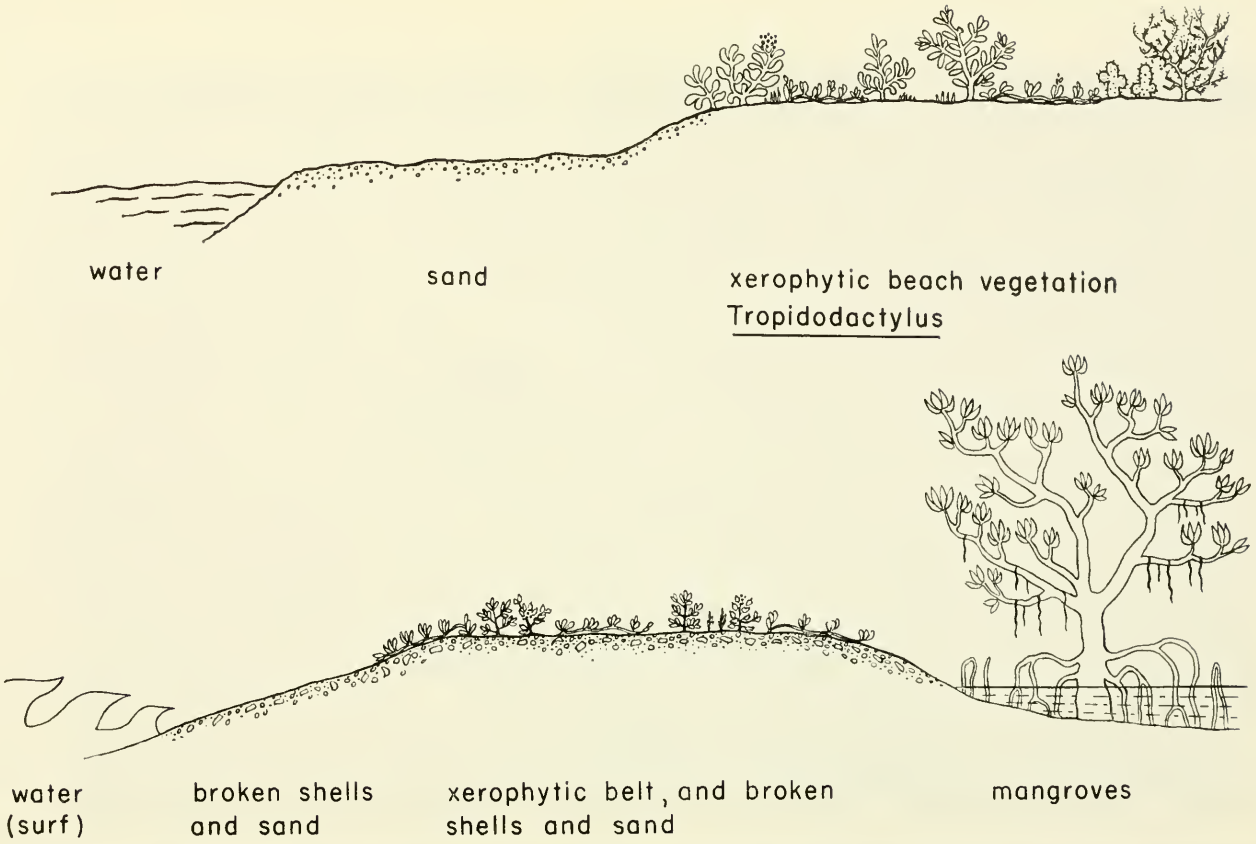

Figure 2. Two characteristic habitats for *Tropidodactylus onca*.

ground. When pursued, the majority of animals observed would merely run among the ground cover. A few specimens, however, were observed to climb the *Mallotonia,* some to a height of 30.0 cm. Their climbing was clumsy and ineffective. The toe structure of this genus is not well adapted for tree climbing. Unlike most anoles, *T. onca* is not arboreal.

Another means of retreat should also be pointed out. At times, a specimen, being pursued, would run into a large hole in the sand opening into a tunnel. Ruthven (1922) also reports this species as escaping into holes. It should be noted, however, that these holes are resting places made by ghost crabs (*Ocypode*) and are not dug by *Tropidodactylus.* It should also be noted that this was a rather infrequent means of escape, used by the lizard only when almost completely exhausted.

At each of the six localities, *T. onca* is found sympatric with *Cnemidophorus lemniscatus lemniscatus.* In those localities (El Agua and Punta los Cocos) where the landward border of the coastal area is occupied by a semi-desertic community, the territory of *Tropidodactylus* partially overlaps that of *Tropidurus torquatus hispidus.* The *Tropidodactylus* penetrate this zone for only a very small distance. In some areas, two other organisms also found sympatric with *Tropidodactylus* are the gecko *Gonatodes vitatus vitatus* and the microteiid *Gymnopthalmus laevicauda.*

Roze (1964) has the following note concerning the diet of *Tropidodactylus:* "The stomach contents examined in various specimens of this species revealed the remains of grasshoppers (Grillidae), Coleoptera, spiders, and various species of Diptera, as well as the remains of other unidentifiable arthropods." *Tropidodactylus* then, like most anoles, is insectivorous. Similarly, like most anoles, the animal is diurnal in its activity. All but one of the twenty-five specimens were captured during the day. The single exception was collected alongside the road near the town El Aguila approximately 2.5 km from Punta de Piedras. It was on a branch of a low bush, *Jatropha gossypiifolia,* in the cleared margin alongside the road. The animal was in typical anole sleeping posture, snout toward the main stem, but with its eyes open. Just prior to being seized, the animal moved its head but did not attempt to flee. This single exception to the otherwise complete coastal distribution of the animals on the island most probably migrated to this inland area along the corridor of low vegetation bordering either side of the roadway. This habitat is ecologically similar to that of the coastal zone.

ACKNOWLEDGMENTS

I am grateful to Dr. Janis Roze and Dr. Ernest E. Williams for critically reading the manuscript and for their valuable suggestions. This study was carried out at the Fundacion La Salle, Margarita Island, Venezuela; I thank Hermano Gines for making the facilities there available to me. Field expenses were partially met by NSF-GY-4183, administered by Manhattan College, and NSF-GB-6944 to Ernest E. Williams.

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BREVIORA

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A NEW SPECIES OF BROMELIAD-INHABITING GALLIWASP (SAURIA: ANGUIDAE) FROM JAMAICA

Albert Schwartz[1]

ABSTRACT. A new species of anguid lizard, *Diploglossus fowleri,* is described from two specimens collected from bromeliads at the northern edge of Jamaica's Cockpit Country. The affinities of the new species are with *D. hewardi* and *D. duquesneyi;* both *D. fowleri* and *D. duquesneyi* appear to be geographic or ecological isolates of the widespread *D. hewardi.*

The Antillean islands of Jamaica and Hispaniola have exceptionally large numbers of species of the anguid lizard genus *Diploglossus* Wiegmann. The latter island has six extant species, whereas Jamaica likewise had six species of which one (*occiduus* Shaw) is presently considered extinct. Cousens (1956) summarized the then-known Jamaican galliwasps and regarded *crusculus* Garman, *barbouri* Grant, *hewardi* Gray, and *duquesneyi* Grant as valid species. Since that time, *D. microblepharis* Underwood has been named from a single specimen from the northeastern Jamaican coast. Cousens (1956), following Grant (1940b), separated the four forms then recognized into two major groups: one group (*crusculus, barbouri*) with short legs and the other (*hewardi, duquesneyi*) with long legs. Schwartz (1970), in discussing *D. occiduus,* suggested that the species *crusculus-hewardi-barbouri-occiduus* might represent a phylogenetic series, despite the interposition in this sequence of both long- and short-limbed species. *D. microblepharis* stands alone; its relationships are with the Puerto Rican *D. pleei* Duméril and Bibron and the Cuban *D. delasagra* Cocteau.

In the summer of 1961, while cutting bromeliads in the deciduous forest at the northern edge of Jamaica's Cockpit Country,

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the extensive karst region in northwestern Jamaica, we secured a single immature galliwasp. Despite the peculiar habitat (no Antillean *Diploglossus* had ever been recorded from bromeliads) the lizard bore resemblances to *D. hewardi,* and it was so considered in the field. Not until 1969, when the paper dealing with *D. occiduus* (Schwartz, 1970) was in preparation, was the lizard re-examined in a routine study of *D. hewardi* for comparative purposes. At that time, the difference in scutellation between *D. hewardi* and the 1961 juvenile specimen quickly became apparent. Further examination of the specimen indicated that, although it resembled *D. hewardi* in general (being a long-limbed form), it differed chromatically and in pattern from that species. But, since it was immature, no further course of action was planned.

It was thus with great pleasure that I accepted the invitation of Dr. Thomas H. Patton of the Florida State Museum to visit Jamaica and stay at Worthy Park Estate during August 1970. Although it was hardly likely that, even with persistent bromeliad cutting, we would encounter another specimen of the arboreal galliwasp, plans were made to revisit the site of capture of the first individual (Windsor, Trelawny Parish). Thanks to the efforts of my assistants and native help, we were successful in securing another and adult specimen of the same form. Study of both individuals convinces me that they represent a new species, related to *D. hewardi,* which has apparently taken to a bromeliad-inhabiting niche — a niche that is virtually unoccupied by Antillean reptiles.

In the summer of 1961, I had the capable assistance of Ronald F. Klinikowski and David C. Leber. Our activities were facilitated by C. Bernard Lewis of the Institute of Jamaica. The 1970 trip was made both pleasant and profitable by the presence of Dale E. Becker, Michael T. Felix, and Danny C. Fowler, whose energy expenditures in bromeliad cutting were noteworthy. In addition, I have examined specimens collected by Richard Thomas in 1967, and by Robert Brenner and Paul Moravec in the same year. All specimens are in the Albert Schwartz Field Series (ASFS) with the exception of the holotype of the new taxon and two specimens of *D. duquesneyi,* which are in the Museum of Comparative Zoology (MCZ) at Harvard University. All measurements are in millimeters and color designations are from Maerz and Paul (1950). I am especially grateful to Dr. Patton for making the Worthy Park facilities available to us, and to Dr. Ernest E. Williams for the loan of the holotype of *D. duquesneyi.*

In honor of Danny C. Fowler, whose endeavors on my behalf can only be recognized in a token fashion by associating his name patronymically with the species, I propose that this bromeliad-inhabiting galliwasp be called

Diploglossus fowleri, new species

Holotype. MCZ 125601, a female, from Windsor, elevation about 500 feet (153 meters), Trelawny Parish, Jamaica, taken 15 August 1970 by Danny C. Fowler. Original number ASFS V19902.

Paratype. ASFS 14421, same data as holotype, 12 July 1961, D. C. Leber.

Diagnosis. An apparently moderately sized (only known adult 105 mm snout-vent length), long-limbed, bromeliad-dwelling galliwasp distinguished from all other Jamaican species by a combination of: 1) low number (101–103) of ventral scales between mental and vent, 2) low number (41–43) of scales around body at midbody, 3) angular subocular scale modally between supralabials 6 and 7, 4) enlarged postmental scale contacting 5 infralabial scales, 5) fourth toe lamellae 18–21, 6) ratio of head width to head length high (80.0), 7) auricular opening small, 8) dorsal trunk and dorsal caudal scales keeled and striate, 9) ventral scales smooth, 10) dorsal pattern of tans and browns arranged in a distinct chevronate pattern, and 11) with dark markings on the head shields.

Distribution. Known only from the type locality.

Description of holotype. An (apparently) adult female with a snout-vent length of 105 mm and tail (almost entirely regenerated) 75 mm; ventral scales between mental and vent 103, 41 scales around body at midbody; fourth toe lamellae 21, angular subocular between supralabials 6 and 7 on one side, between 7 and 8 on the other; head length 18.5, head width 14.8; ratio of head width to head length 80.0; median enlarged postmental (= first unpaired chin shield) small and contacting 5 infralabials. In life, dorsal pattern consisting of a series of about 16 or 17 wood brown chevrons, their apices pointing posteriorly, from the neck to the sacrum, on a tan ground; sides with somewhat lighter brown continuations of these chevrons both on the neck and between the limbs, the lateral continuations forming a series of more or less vertical brown bars which extend ventrad to about the level of the limb insertions; a few scattered paler tan dots or

flecks in two vague lateral horizontal rows, associated with the lateral brown vertical bars; head tan, with more or less symmetrical wood brown markings (a pair on the snout, an unpaired median blotch in the preorbital region, a median unpaired blotch on the posterior portion of the frontal, and the interparietal-parietal region with the scales dark edged); a black preorbital line on the lores; temples longitudinally streaked with very dark wood brown; a series of three brown lines on the supralabials, one below the eye, the two others extending vertically across the supralabials in the loreal region, all continuous ventrally across the infralabials; a series of three very dark brown to black nuchal blotches, the posteriormost the largest and located above the insertion of the forelimb; limbs mottled brown and black dorsally, the forelimbs additionally with some intermixed tan areas and consequently appearing more mottled or marbled than the hindlimbs; underside pale orange, with discrete brown longitudinal streaks (four scales in length) or flecks on throat, and deep orange streaks on venter; underside of limbs and tail (unregenerated portion) pale orange; iris brown with orange pupillary ring.

Variation. The paratype is a juvenile lizard with a snout-vent length of 66 mm. Scale counts are: 101 scales between mental and vent, 43 scales at midbody, angular subocular between supralabials 6 and 7 on one side, between 8 and 9 on the other, fourth toe lamellae 18; head length 12.7, head width 9.3 (ratio 73.2). In life, the paratype was tan (Pl. 14G6) dorsally with about 18 dorsal chevrons between the neck and the sacrum; the sides were paler tan (Pl. 13D3). The snout was olive, with the jowls and the base of the tail slightly reddish. The limbs were tan, spotted with dark brown to black. The venter was translucent gray, marbled with brown on the throat, and marked with reddish on the trunk and underside of the hindlimbs and tail. The facial markings, described for the holotype, were equally as prominent in the juvenile paratype. The dorsal chevronate pattern was dark brown to black, and on the sides the chevrons were continuous with weakly defined lateral vertical brown bars, each of which was followed by a creamy bar. Three nuchal-supra-axillary blotches were black, and the frontal head shield had a dark anterior margin with some additional dark suffusions on the dorsal surface of the head. The postmental scale in the paratype is very small, but it contacts 7 infralabials; the contact on the right side

between the postmental and the third infralabial is slight, but the contact on the left side is slightly more broad.

Comparisons. D. fowleri needs comparison only with the three long-limbed Jamaican species (*occiduus, hewardi, duquesneyi*). The new species differs from the short-limbed *crusculus* and *barbouri* in having much larger limbs and from *microblepharis* in having the frontal longer than broad (in *microblepharis,* the frontal is broader than long). Counts of ventral scales (101–103) in *fowleri* overlap (of the other species) only the counts of *crusculus* (97–122, data from Grant, 1940b); all other Jamaican species combined have ventral counts ranging from 107 to 150, with the low count of 107 in the giant *occiduus,* the high count of 150 in *barbouri.* In midbody scales, *fowleri* (41–43) overlaps only *crusculus* (36–49) and *microblepharis* (43). Combined midbody counts for all other Jamaican species (with the exception of *crusculus* and *microblepharis*) vary between 47 (*barbouri*) and 59 (*hewardi*). In having the angular subocular between supralabials 6 and 7, *fowleri* resembles *barbouri* and *crusculus* but differs from *hewardi* and *duquesneyi* (7 and 8), *microblepharis* (5 and 6), and *occiduus* (8 and 9).

In *fowleri,* the dorsal scales are striate and keeled; this condition occurs in all other Jamaican galliwasps with the exception of *occiduus* (dorsals striate but not keeled). In having smooth ventrals, *fowleri* resembles *barbouri, hewardi, occiduus,* and *microblepharis.* The ventral scales are striate in *crusculus* and *duquesneyi.* Note, however, that *hewardi* may have weakly striate ventrals, and *duquesneyi* may have smooth ventrals. Finally, the striate and keeled dorsal caudal scales of *fowleri* are like those of *crusculus* and *duquesneyi;* all other Jamaican species have smooth (*hewardi, occiduus*) or keeled (*microblepharis*) superior caudals. From the above summary, it is obvious that *fowleri* combines features of scutellation of several Jamaican species in new and different ways, and that the new species differs in combination of these characteristics from all other Jamaican species.

Presumably, as will be noted below, *D. fowleri* is a local derivative of the widespread *D. hewardi.* The fact that the juvenile *fowleri* was, in the field, considered as *hewardi* suggests the similarities between the two species. However, in addition to the structural differences noted in the above paragraph, the two species differ strikingly in coloration in life and perhaps less so in

dorsal pattern. More importantly, the size of the auricular opening in *fowleri* is much the smaller; comparison of the opening in the *fowleri* holotype and a similarly sized *hewardi* (ASFS 14892; female with snout-vent length of 109 mm) reveals, even upon casual inspection, that the auricular opening of *fowleri* is slightly more than half the size of that of the *hewardi*. In addition, the two species differ in that *fowleri* has larger ventral scales (101–103 between mental and vent in *fowleri,* 113–135 in *hewardi*), and fewer scales at midbody (41–43 versus 49–59 in *hewardi*). The enlarged postmental contacts 7 infralabials in all *hewardi* examined, whereas at least in the *fowleri* holotype this scale contacts only 5 infralabials (weak contact with 7 infralabials in the paratype). In *fowleri,* the angular subocular modally lies between supralabials 7 and 8, whereas in *hewardi* it lies between supralabials 6 and 7. *D. fowleri* exceeds *D. hewardi* in number of fourth toe lamellae (15–19 in 22 *hewardi,* 18 and 21 in two *fowleri*). Finally, the head width/head length ratio in adult female *hewardi* varies between 70.7 and 74.1, whereas in the *fowleri* holotype, this ratio is 80.0. There are no comparably sized juvenile *hewardi* for comparison of this ratio in the paratype of *fowleri,* but the ratio (73.2) in this specimen lies near the upper extreme of ratios in *hewardi* with shorter snout-vent lengths (45-52 mm; ratios 66.4 to 73.8).

The dorsal coloration of *hewardi* has been repeatedly recorded as greenish brown to greenish tan, but some individuals have the dorsum very dark brown (almost black) to metallic tan. The head regularly is unmarked dorsally, and vertical subocular and loreal lines are absent. The dorsal pattern consists of a transverse series of confused bars or bar fragments; these pattern elements are usually so broken that no meaningful count can be taken. There is a strong tendency for the *hewardi* dorsal pattern elements to consist of bars, rather than chevrons as in *fowleri.* Perhaps the most distinctive pattern feature of *hewardi,* in contrast to *fowleri,* is that of the throat. In *hewardi,* the throat has a broad dark reticulum, the pattern extending as far posterior as the forelimb insertions. This pattern is expressed even in the smallest juveniles and becomes more intense with increasing size. No *hewardi* has the discrete brown throat lines and flecks of *fowleri.* In addition, the ground color of the throat in *hewardi* is often blue to purplish, not pale orange as in *fowleri.* The deep orange belly markings of *fowleri* are absent in *hewardi;* some

hewardi have belly markings that are not discrete as in *fowleri* and are gray in life.

Comparisons in detail with *D. occiduus* are hardly necessary. In addition to the scutellogical differences noted above, the huge size of *occiduus* (to 305 mm snout-vent length) and its presumed terrestrial habits, coupled with its general bulk, immediately distinguish it from *fowleri.*

The only other long-limbed Jamaican galliwasp is *D. duquesneyi.* Scutellogical differences have already been noted between this species and *fowleri.* I have examined the holotype (MCZ 45194) and one other specimen (MCZ 45181) of *duquesneyi.* The species was casually defined by Grant (1940a: 6) on the basis of one juvenile specimen, and Cousens (1956) gave additional pigmental and pattern differences between two specimens of *duquesneyi,* and *hewardi.* I have examined the two extant *duquesneyi* and both are damaged about the body so that accurate scale counts are difficult. Ventral scales between the mental and vent are about 116 and 122, midbody scales are about 48 and 49, and fourth toe lamellae are 19 and 23. The angular subocular lies between supralabials 7 and 8 on both sides of both specimens. *D. hewardi* and *D. duquesneyi* are comparable in dorsal pattern: the transverse markings in both are distinctly straighter and more barlike than the chevronate pattern in *fowleri.* In addition, comparison of equally sized *hewardi* and *duquesneyi* shows that *duquesneyi* (like *fowleri*) has a larger auricular opening than *hewardi.*

D. fowleri differs from *D. duquesneyi* in that the former has fewer ventrals between mental and vent (101–103 versus 116–122), fewer midbody scales (41–43 versus 48–49), the angular subocular between supralabials 6 and 7 rather than between 7 and 8, and smooth rather than striate ventrals (although the holotype of *duquesneyi* has smooth ventrals). Two pattern elements differentiate *duquesneyi* from *fowleri:* the former has the tail (at least in juveniles) banded alternately black and sky blue (Grant, 1940b: 106), a feature unknown in any other Antillean galliwasp, and *duquesneyi* has an immaculate throat and venter (color unknown), a feature that separates *duquesneyi* from both *fowleri* and *hewardi. D. duquesneyi* also lacks the prominent facial markings of *D. fowleri.* Finally, the head width/head length ratio ($\times$ 100) in *duquesneyi* is much less than this ratio in both *fowleri*

and *hewardi*. In an apparently subadult female *duquesneyi* with a snout-vent length of 96, the HW/HL ratio is 69.8, below that of similarly sized female *hewardi* (ratios 70.7–73.7) and much below that of the slightly larger female holotype of *fowleri* (80.0). The HW/HL ratio in the juvenile holotype of *duquesneyi* (snout-vent length about 65) is 66.4, whereas this ratio in the *fowleri* paratype (snout-vent length 66) is 73.2; the HW/HL ratio in the *duquesneyi* holotype falls at the lower extreme of this ratio in smaller *hewardi* (ratio 66.2 to 67.3 in *hewardi* juveniles with snout-vent lengths of 49 to 52).

Interestingly, Richard Thomas noted that a *D. hewardi* from Darliston, Westmoreland Parish, in western Jamaica, (and far removed from the known range of *D. duquesneyi,* which has been taken only on Portland Point, Clarendon Parish, in south-central Jamaica) with a snout-vent length of 48 mm, had pale blue distal tail bands alternating with brown bands. There seems little doubt that *hewardi, duquesneyi,* and *fowleri* are closely related, and that *duquesneyi* and presumably *fowleri* are peripheral geographic satellite species derived from parent *hewardi* in special situations.

Remarks. The two specimens of *D. fowleri* were collected under the following circumstances. Both specimens were taken from bromeliads along the edge of the steep trail from Windsor Great House to Windsor Cave and thence up the escarpment of the Cockpit Country. In the case of the holotype, a Jamaican had been hired to cut arboreal bromeliads and had climbed a tall tree of moderate girth (0.5 meters) just below the path in deciduous forest. He had cut all but the last one or two bromeliads when the galliwasp rapidly descended the trunk of the tree and paused in confusion on a leaf about six feet above the ground. There is no doubt that the animal had been disturbed from its diurnal retreat by the chopping of adjacent bromeliads and had decided to abandon its place of retirement. The small paratype was taken from the moist center of a bromeliad that had been growing 2.5 meters above the ground. When the bromeliad was cut and thrown onto the narrow path, the lizard was found inside the whorls of leaves. In both cases, the adjacent area was well forested. The elevation along the path is about 500 feet (153 meters).

The Jamaican Cockpit Country is a karst region in northwestern Jamaica. Its extent is about 20 miles (32 kilometers) east-west and about 10 miles (16 kilometers) north-south; the region centers in Trelawny Parish but extends for short distances

into St. James Parish on the west and St. Elizabeth and Manchester parishes to the south. No roads penetrate it, but a series of peripheral roads allows some ingress into the region. An exception is a relatively newly constructed road north of Quick Step on the southern border of the Cockpit, where penetration of about five miles (8 kilometers) is possible into virtually virgin territory.

In search of *Sphaerodactylus* and hylid and leptodactylid frogs, we cut both terrestrial and arboreal bromeliads in several regions associated with the Cockpit periphery and elsewhere: between Spring Vale and Mulgrave (St. James and St. Elizabeth parishes), between Stonehenge and Burnt Hill (Trelawny Parish); south of Moneague on Mt. Diablo and west of Lluidas Vale (St. Catherine Parish), in the Dolphin Head region between Askenish and Town Head (Hanover and Westmoreland parishes), between Plum Park and Garlands (St. James Parish), and between Raheen and north of Quick Step (Trelawny Parish). In no case did we secure *D. fowleri,* although a single *D. crusculus* was secured from a terrestrial bromeliad north of Cave in Westmoreland Parish. The possibility remains that *D. fowleri* is not an obligate inhabitant of bromeliads, and that it is a terrestrial galliwasp that, in the pitted, pocked, and rock-strewn Cockpit Country, finds diurnal sanctuary in terrestrial situations from which it would be a lucky collector indeed who would secure it. On the other hand, there is no evidence to controvert the apparent fact that *D. fowleri* is indeed a bromeliad dweller and that it occurs in no other situation. If such is the case, it must be either extremely uncommon, remarkably elusive, or ecologically or altitudinally restricted in some presently unknown fashion. Along these lines, see Underwood's (1959: 1) comments on his inability to secure a second specimen of *D. microblepharis.* The fact that the area where the *microblepharis* was secured backs upon limestone hills suggests, as Underwood stated, that it may have wandered from its usual habitat into a situation where it was fortuitously secured with relative ease.

Diploglossus fowleri is not known to be sympatric with any other species of galliwasp. However, *D. hewardi* has been taken 1.5 miles NW of Windsor, and *D. crusculus* has been secured 3.0 miles NW of Windsor — both in terrestrial situations. In addition, *D. barbouri* has been collected along the eastern margin of the Cockpit Country between Stonehenge and Burnt Hill. The

lack of precisely sympatric records between *fowleri* and any of these three species is not surprising, since, as pointed out above, collecting galliwasps within the Cockpit Country itself is a difficult and well-nigh impossible task except in especially favorable localities. If *fowleri* is truly bromeliadophilous, then it may in places be syntopic with *D. crusculus*, but such syntopy remains to be encountered.

As presently understood, then, *D. fowleri* is a bromeliad-inhabiting galliwasp that is presumably limited to the Cockpit Country area and possibly to lower elevations in that region. It is rather surprising that the bromeliad niche has been so neglected by Antillean reptiles, in contrast to Antillean amphibians. Certainly Jamaica has the highest share of bromeliadicoles, both amphibians and reptiles; in addition to *D. fowleri, Hyla brunnea, H. wilderi, H. marianae,* and *Eleutherodactylus jamaicensis* are obligate bromeliad dwellers, and several other frogs (*E. grabhami, E. cundalli, E. pantoni*) are encountered with regularity in terrestrial bromeliads. Among reptiles, *Sphaerodactylus oxyrhinus* appears to be confined to this situation, and a new species of *Sphaerodactylus,* to be described by Richard Thomas, likewise is thus limited in habitat. *S. argus, D. crusculus,* and *Tropidophis haetianus* are encountered in bromeliads upon occasion. This list of both obligate and facultative bromeliadicoles far exceeds that from any other Antillean island. On the other hand, no one has systematically cut arboreal and terrestrial bromeliads elsewhere than on Jamaica. It seems likely that this is a niche that will well repay investigation on other Antillean islands.

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THE PALEONTOLOGY AND EVOLUTION OF CERION II: AGE AND FAUNA OF INDIAN SHELL MIDDENS ON CURAÇAO AND ARUBA

Stephen Jay Gould

ABSTRACT. *Cerion uva* has been found in great abundance in three Meso-Indian (preceramic) shell middens on Curaçao. Shells from all three sites yield radiocarbon ages of about 4000 years B.P. Different groups of Meso-Indians from Venezuela reached Curaçao and the nearby island of Cubagua at about the same time. A Neo-Indian (ceramic) midden on Aruba is approximately 1500 radiocarbon years old. Lists of the molluscan fauna from all sites contain only intertidal and shallow water species. Collecting areas can be specified by noting differences among sites in the presence of species from various environments (rocky intertidal, mangrove, shallow grassy and shallow rocky).

In the shell middens, *Cerion* presents two outstanding features: 1) almost all shells have had the apical whorls removed artificially and, 2) shells are larger than any living today. The apical whorls were removed by striking; flint tools found at the sites accomplish this task easily. This was done to release the internal vacuum and allow the animal to be sucked out through the normal aperture. Larger shells might indicate, since modern *Cerion* is so phenotypically variable, that the climate of Curaçao 4000 years ago was more moist (and therefore more hospitable) than today. But there is no independent evidence for more rainfall at that time. If the effect is mainly genetic, these shells might come from relict populations, adapted to the pluvials of the previous glaciation. *Cerion uva* has been found in a shell midden in Venezuela; this establishes the reciprocity of trade between mainland and offshore islands.

INTRODUCTION

Only a few mollusks have won entry into the Papiamento language of the Dutch Leeward Islands. These are mostly edible species — *kiwa* (*Cittarium pica*), *karko* (*Strombus gigas*), and *tapa koncha* ("cover shell" — a general name for chitons). Yet

Cerion uva, the ubiquitous pulmonate of these islands, stands out for the plethora of names attached to it, names that distinguish small from large and beach from bush. Nevertheless, *Cerion* plays almost no role in the economy of these islands today — though one of its names, *kokolishi kalakuna* (turkey shell), reflects the fact that it is sometimes fed to turkeys as a source of lime. It is never eaten, save as an aphrodisiac by some older residents who believe that sea shells preserve sexual potency (and do not realize that this halophilic pulmonate, which lives just landward of *Tectarius muricatus,* does not come from the sea). But to another people, the original Indian inhabitants of Curaçao, *Cerion uva* was a major source of food, for the oldest middens of the island are crammed with their shells.

Of the many shell sites that have been studied (Van Heekeren, 1960: 103–109, for review of archaeological work and Van Heekeren, 1963), *Cerion* is known only from the older, preceramic middens of Curaçao. Whenever it occurs, it presents two peculiarities: shells are far larger than the largest living *C. uva,* and most all have had the apical whorls removed artificially.

Thanks to the kindness of Father Paul Brenneker and Mr. Elis Juliana, local collectors, folklorists, and historians (and my informants for the opening paragraph), and Dr. F. Creutzberg, Director of the Biological Station at Piscadera Baai, Curaçao, I had the opportunity to study the shell sites during the summer of 1968. In this paper, I shall review the archaeological setting of these islands, report on radiocarbon dating of the shell sites, tabulate the fauna of each and present environmental interpretations, and discuss the occurrences of *Cerion* with special reference to the peculiarities mentioned above.

CARIBBEAN PREHISTORY AND DESCRIPTION OF SITES

The Dutch Leeward Islands are tied, geographically, to Venezuela. Aruba, only 27 km from the mainland, lies on the coastal shelf, in easily navigable waters. Curaçao and Bonaire are more distant (64 and 87 km respectively), and the passage is deeper (up to 1500 m) and more treacherous (Van Heekeren, 1960: 103). The early colonization of these islands must be discussed in the context of Venezuelan archaeology (Cruxent and Rouse, 1958–59, 1969; Rouse and Cruxent, 1963; Rouse, 1960, 1964, 1966).

The Pre-Columbian inhabitants of Venezuela and the Caribbean are designated Paleo-, Meso-, or Neo-Indians on the basis of technology and inferred economy. Although the three stages do express a chronological progression, none of their artifacts function as "index fossils" in establishing contemporaneity throughout the Caribbean, for the traits of a new stage are attained at different times by different peoples. There were, for example, still some preceramic Meso-Indians on Haiti and Western Cuba when Columbus arrived (Rouse, 1966).

The original inhabitants of the New World were Paleo-Indians, "hunters of mammoths and other large land mammals" (Rouse, 1966: 125). Their stone tools have been found in Venezuela and designated as markers of the Joboid Series. They date, approximately, from 17,000–7,000 B.P. The oldest radiocarbon date for Joboid charcoal is 16,870 years B.P. (Rouse and Cruxent, 1963). In earlier works, Cruxent and Rouse held that Paleo-Indians were not sea-farers, but Paleo-Indian sites have recently been found at Mordán in the Dominican Republic and dated to at least 4560 radiocarbon years B.P. They believe, moreover, that the Mordán site is predated by another at Casimira that may be as much as 7,000 years old (Cruxent and Rouse, 1969). Although the mainland source of these first Hispaniolans is not known, these finds indicate that some Paleo-Indians crossed considerable stretches of ocean, probably on rafts and by accident (Cruxent and Rouse, 1969).

Much scholarly agitation of late has been directed to the issue of whether or not Paleo-Indians were responsible for the extermination of large land mammals (Martin and Wright, 1967). In any event, their demise drew our pre-agricultural people to the sea and inaugurated Meso-Indian culture, characterized by "relatively few stone tools. Projectile points are made of bone rather than stone and shell artifacts are common, reflecting the maritime orientation" (Rouse, 1966: 126). Meso-Indian artifacts in Caribbean Venezuela belong to the Manicuaroid Series and date, approximately, from 7,000 to 3,000 years B.P. The oldest radiocarbon date for mainland Venezuelan Meso-Indians is 5750 B.P. (Rouse and Cruxent, 1963). There is an extensive Meso-Indian site on Cubagua, another of Venezuela's offshore islands. Charcoal from the base of this deposit dates at 4275 radiocarbon years B.P.

The subsequent Neo-Indian culture is "marked by pottery making and fully developed agriculture" (Rouse, 1966: 126). The invention of pottery was the crucial archaeological event that inaugurated the Neo-Indian period; therefore Meso-Indian and earlier sites are often designated simply as "preceramic." Agriculture, with manioc as a staple crop, and pottery were developed in the Orinoco Valley during the 2nd millennium B.C. During the 1st millennium B.C., some Neo-Indians moved out to the coast and became sea-farers. Displacing Meso-Indians as they went, they migrated to the coastal islands, up the Lesser Antilles and reached the Greater Antilles ca. 250 A.D. and the Bahamas ca. 1000 A.D. This displacement was still occurring when Columbus reached the New World (Cruxent and Rouse, 1969).

The *Cerion* sites of Curaçao are all Meso-Indian in nature. I studied the following three sites:

1. Rooi Rincón — North coast, west of Hato Airfield; in soil at the base of a small cave in a raised Pleistocene reef that also houses the larger cavern of Hato and several others; approximately 40 m above present sea level and 1 km from the coast. This well-known site was excavated by Cruxent in 1965 (Tamers, 1967) and by Van Heekeren in 1960 (Van Heekeren, 1963). Crudely chipped stone tools and flint flakes are common but, after digging for 14 days, Van Heekeren found only one other artifact, a shell disc bead (Van Heekeren, 1963: 5). The naturally broken columellar tips of *Strombus gigas* are similar in form to some of the fashioned shell gouges common in the Manicuaroid deposits of Cubagua (Cruxent and Rouse, 1958–59); they may have been used for digging meat out of shells. Many other natural objects could have been used as tools. Particularly suspect are the smoothly eroded and fairly pointed branches of the stag horn coral, *Acropora cervicornis,* that are fairly common at this site and at Kintján (site 2). These, obviously, have no nutritional value and must have been carried to the site for some other purpose. Other objects, land crab claws for example, might have been used for digging meat from shells after their own contents had been consumed. I found a few bits of charcoal: some of the shells are strongly scorched. Cruxent says of this deposit: "A Meso-Indian complex of collectors with industry of stone chips. Classified as a marginal development of El Jobo. No archaeologic station of this type presently known in Venezuela" (*in* Tamers, 1967: 244).

2. Kintján — Near south coast, east of Willemstad. The area, a hillslope, is being cleared for construction and shells are loose at the surface; their presence in a small area indicates original concentration in a coherent deposit. Flint chips and crude stone tools are, as at Rooi Rincón, common at this site.

3. Tafelberg — Near south coast, just east of the Tafelberg Santa Barbara. Only a few shells could be collected from the recently blasted rubble of these phosphate workings. Mr. Harry Evers, engineer at the Tafelberg phosphate workings, informs me that, prior to the blasting, the shell heap was a coherent deposit with two layers, marine shells at the base and decapitated *Cerion* at the top. I found no artifacts at this much disturbed site.

Dr. P. Wagenaar Hummelinck, pre-eminent natural historian of these islands, has told me (personal communication, 1970) of one additional *Cerion* locality at Hato Cave; I have not seen this site. He also states that he knows of no other *Cerion* site on any of the three islands.

For comparison, I add to the *Cerion* sites of Curaçao one later, Neo-Indian deposit from Aruba:

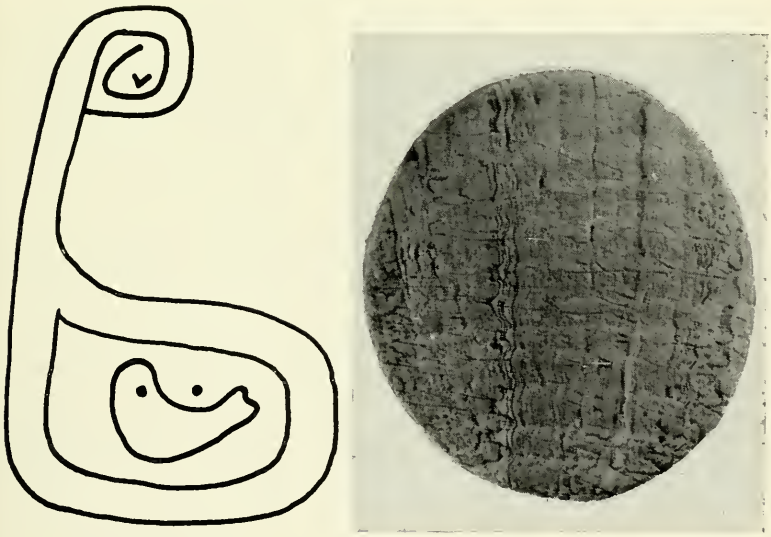


Figure 1. Artifacts from Ceru Canashito, Aruba.
1a) left: rock drawing, presumably depicting a pregnant woman.
1b) right: shell disc made from *Melongena melongena*. Actual height: 43 mm.

4. Ceru Canashito — North slope of this limestone terrace. I chose this among the many Neo-Indian sites of Aruba for two of its outstanding features. Good skeletal material has been collected from the caves near its summit (Tacoma, 1959), and these caves contain some of the best of the celebrated and mysterious rock paintings of these islands (Hummelinck, 1953, 1957). One of these, probably depicting a pregnant woman, is reproduced as Figure 1a. (There is, of course, no reason to assume that the rock drawings are contemporaneous with the shells; Van Heekeren (1960), in fact, suspects that they were fashioned by Meso-Indians and venerated by later inhabitants.) Shells occur at all levels of the slope, but are concentrated by gravity at the base in an inhomogeneous deposit. Sherds of a coarse, unornamented, grit-tempered pottery are common. Shell artifacts include the columellar points of *Strombus gigas* and the unperforated shell disc, made from the outer whorl of *Melongena melongena,* shown in Figure 1b. Such unperforated shell discs are common on the islands; their function is unknown (Van Heekeren, 1960: 112).

AGE OF THE SHELL MIDDENS

Tamers (1967) reported the first radiocarbon dates from archaeological sites in the Dutch Leeward Islands; all samples were charcoal and all were supplied by Cruxent. Included are five dates for the Rooi Rincón shell midden, two from a pit previously excavated by Van Heekeren and three from two new pits. The dates range from 3900 $\pm$ 50 to 4490 $\pm$ 60 with a mean of 4194 radiocarbon years (see Stuiver and Suess, 1966 on the relationship between radiocarbon and calendar years). These are the only dates previously calculated for preceramic sites on these islands.

Radiocarbon ages were determined for 11 shell samples by Geochron Laboratories, Inc., Cambridge, Massachusetts (*Chama macerophylla* and *Cittarium pica* from each of the five sites and *Anadara notabilis* from Ceru Canashito). "The shells were cleaned of foreign material and were thoroughly leached with dilute HCl in an ultrasonic cleaner to remove the surficial layer of carbonate and expose fresh material. The cleaned shells were then hydrolyzed to recover CO_2 for the analysis" (personal communication from H. W. Krueger of Geochron). Dates are based on a half-life of 5570 years and referenced to 1950 A.D.

Dates based on shells are not as reliable as those determined for pure carbon (charcoal), for $CaCO_3$ is often altered by percolating, acidic groundwaters. I was anxious to determine the correspondence between shell and charcoal dates for Rooi Rincón; I found no charcoal at any of the other sites. All dates are shown in Table 1.

The correspondence at Rooi Rincón is satisfactory, and all preceramic sites of Curaçao are about 4000 radiocarbon years old. This date is particularly interesting since it corresponds so well with the base of the great Meso-Indian site at Punta Gorda, Cubagua Island (p. 21). The artifacts of this Cubagua complex of the Manicuaroid series differ greatly from those of Rooi Rincón (Cruxent and Rouse, 1958–59) and we must assume that different groups of Meso-Indians from Venezuela colonized the coastal islands at about the same time.

The great spread of dates for the Neo-Indian site of Ceru Canashito can be explained in two ways. It is a very inhomogeneous deposit of shells artificially concentrated at the base of a slope and may represent a long span of habitation. Alternately, the *Cittarium* date could be spuriously young. *Cittarium* has been and remains a staple food of the islands. The *kiwa* is sold at all native market places; shells are carried and discarded all over the island. If this date has been falsified by the inclusion of a fairly modern shell, then the Canashito midden may represent a more coherent deposit, about 1500 radiocarbon years old.

FAUNA OF THE SHELL MIDDENS

In presenting these faunal lists, I have excluded the micromolluscs that could have played no role in the economy of the Indians (though *Truncatella* and other rissoids are reasonably common as accidental transports). In each site, there are a few species that clearly dominate; these are merely listed as common. Numbers of specimens are given for other species. I have used Warmke and Abbott (1961) and Coomans (1958) as guides to identification; order of listing and family allocations follow the former source.

1. Rooi Rincón

AMPHINEURA

Acanthopleura granulata — common

GASTROPODA PROSOBRANCHIA

TROCHIDAE

Cittarium pica — common

TURBINIDAE

Astraea tecta — 1

Astraea tuber — 1

NERITIDAE

Nerita peloronta — 11

Nerita versicolor — 6

Nerita tesselata — 4

LITTORINIDAE

Nodilittorina tuberculata — 4

Echinus nodulosus — 1

Tectarius muricatus — 10

VERMETIDAE

Petaloconchus mcgintyi — 3

STROMBIDAE

Strombus gigas — 4 apices and 3 columellas

MURICIDAE

Murex brevifrons — 8

MAGILIDAE

Coralliophila abbreviata — 2

Coralliophila caribbea — 1

FASCIOLARIIDAE

Leucozonia nassa — 1

XANCIDAE

Vasum capitellum — 1

GASTROPODA PULMONATA

CERIONIDAE

Cerion uva — common; 18 of 129 specimens have intact apices

BIVALVIA

ARCIDAE

Arca zebra — 12 valves

Arca imbricata — 4

Anadara notabilis — 4

MYTILIDAE

Brachidontes exustus — 2

PTERIIDAE

Pinctada radiata — 13

PECTINIDAE
Pecten ziczac — 2
LIMIDAE
Lima scabra — 10
OSTREIDAE
Ostrea frons — 12
Crassostrea rhizophorae — 9
CHAMIDAE
Chama macerophylla — common
Pseudochama radians — 2

Nonmolluscan remains: a few branches of stag-horn coral (*Acropora cervicornis*), land crab claws (common), a few barnacles, fish bones and a small fragment of an echinoderm test.

Not all these animals were eaten. Many, especially among the snails, are small and rare at the site (turbinids, magilids, fasciolariids, and xancids); others (*Petaloconchus* and barnacles) cement to other shells and surely won a free ride on their edible hosts (probably *Chama*).

The main food sources were the land snail *Cerion,* land crabs, intertidal chitons, the intertidal and just subtidal snail *Cittarium* and the shallow water clam, *Chama;* all are very abundant and easily gathered. Less common but still important as food sources are the conch *Strombus gigas, Nerita peloronta,* and *Murex brevifrons* among the snails (the last two artificially broken in characteristic ways — Figs. 2 and 3) and arcids, oysters, and limids among the clams.

The shells provide an excellent picture of the environment from which they were gathered. All the major intertidal rock-clingers are represented (all three common West Indian *Nerita,* chitons, and the famous homeomorphic series *Nodilittorina-Echinus-Tectarius*). These species inhabit rocky shores in areas of active surf. All other species can be found in less than 10 feet of water on a varied bottom containing reefy and rocky areas (*Chama, Arca, Lima*) and stretches of sand and grass (*Anadara, Strombus*). There may have been a lagoon with mangroves nearby, for many important elements of the mangrove-root community are present (*Murex brevifrons, Ostrea frons, Crassostrea rhizophorae,* and *Brachidontes exustus*).

Van Heekeren (1963) stated, correctly no doubt, that the shells were collected on the nearby north coast (Fig. 4b). Since

Figure 2. *Murex brevifrons* shells from Kintján (left) and Rooi Rincón (right). Note characteristic breakage pattern in both. This can be achieved by placing the shell face down upon its aperture and striking the apex. Actual height of Kintján specimen: 54 mm.

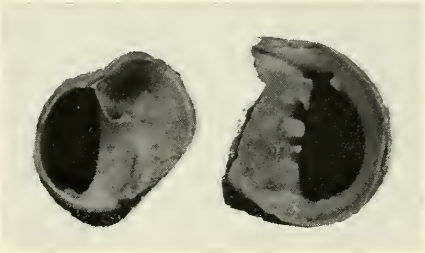


Figure 3. Neritids from Rooi Rincón broken in characteristic fashion. Left: apertural portion from rear; Right: apertural portion from front. Such a break is made by placing the shell face down upon its aperture and striking the body whorl with a blunt object. This is also the natural breakage pattern in most cases. Right-hand fragment is 18 mm high.

the unremitting trade winds blow against this coast (producing a strong surf most unconducive to shell gathering), Van Heekeren suggested that sea level at this earlier time was 6–7 m higher than today. This would submerge the extensive raised reef that forms the lower terrace all around Curaçao and produce a broad area of calmer, shallow water. (And from the supposed extent of this change in level, he postulated a great age for the deposit and classified it, tentatively, as Paleo-Indian.) This hypothesis of a major shift in sea level is unnecessary for two reasons: 1) With an age of 4000 radiocarbon years, any eustatic fall in level is ruled out; if anything, mean sea level then was a bit lower than today (Redfield, 1967; Milliman and Emery, 1968). This leaves tectonic uplift. Curaçao has, indeed, been uplifted during the Pleistocene (the oldest terrace, atop the Tafelberg, lies at 140–200 m, but 7 m in 4000 years is not likely). 2) The trade winds do produce a strong surf along the north coast. But Rooi Rincón lies on that part of the coast that runs due east-west; here the winds run along the coast and the waters are fairly calm. Modern *Cerion* populations illustrate the climatic results of changes in coastal direction. *Cerion* lives atop the first terrace all along the coast. In areas continually buffetted by the strong dry wind, they aestivate for much of their lives and remain small as adults; they grow bigger in calmer areas. A graph of *Cerion* size vs. distance from Westpunt (Fig. 4a) is a good map of coastal direction (Fig. 4b). *Cerion* is small where the coast runs north-south and large where it runs east-west. They reach their greatest size at Rooi Rincón. Thus, Rooi Rincón lies in the only area of Curaçao that provides good conditions for shell gathering on the north coast.

2. Kintján

GASTROPODA PROSOBRANCHIA

TROCHIDAE

Cittarium pica — common

STROMBIDAE

Strombus gigas — common

CYMATIIDAE

Charonia variegata — 1

MURICIDAE

Murex brevifrons — 3 (broken as at Rooi Rincón, Fig. 2)

MELONGENIDAE
Melongena melongena — 2

GASTROPODA PULMONATA
CERIONIDAE
Cerion uva — common, 7 of 347 specimens have intact apices

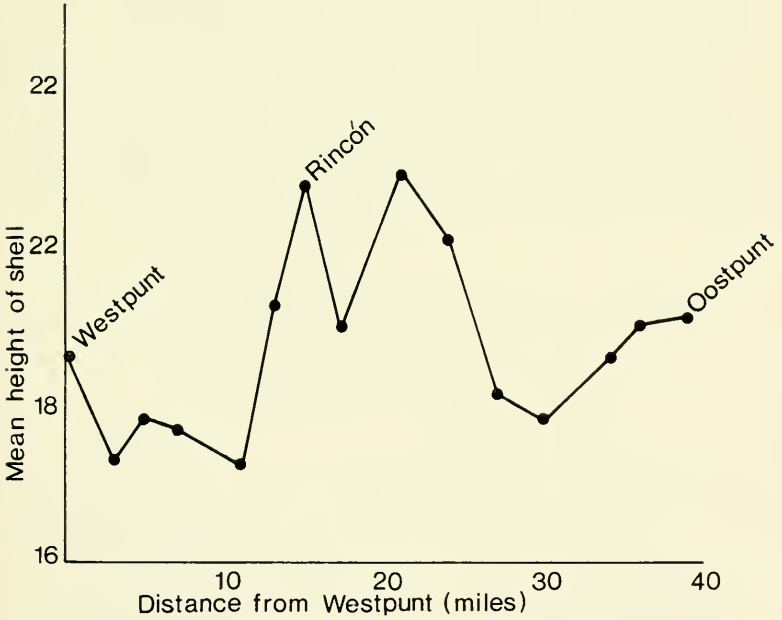
BIVALVIA
ARCIDAE
Arca imbricata — 13
Barbatia cancellaria — 3
Anadara notabilis — common
PTERIIDAE
Pinctada radiata — 3
PECTINIDAE
Pecten ziczac — 7
LIMIDAE
Lima scabra — 6

Figure 4. Correlation of coastal direction and shell size.
4a) left: map of Curaçao. 1. Rooi Rincón at point where coast runs east-west. 2. Kintján. 3. Tafelberg. 4. Schottegat (where shells at Kintján were collected).

OSTREIDAE
Ostrea frons — 7
Crassostrea rhizophorae — 6
CHAMIDAE
Chama macerophylla — common

Nonmolluscan remains: branches of stag-horn coral (*Acropora cervicornis*), barnacles, and fish bones.

The shallow water fauna of Kintján is very similar to that of Rooi Rincón, both in species composition and order of dominance (*Chama* and *Cittarium* followed by *Strombus,* arcids, oysters, and limids). Since shells are not so common at Kintján, several species, rare and unimportant at Rooi Rincón, are not found here.



4b) right: Mean shell heights (20 adults per sample) for local populations living in similar microhabitats directly on the first terrace along the east coast of Curaçao. Shells are largest where trade winds do not hit coast directly.

I found no land crabs at Kintján, but *Cerion uva* is even more common here than at Rooi Rincón. There is, however, one outstanding difference between the two sites: there are no intertidal rock-dwellers at Kintján (neritids, littorinids, or chitons), while all the common forms are found at Rooi Rincón. This difference permits us to specify the collecting area for Kintján shells.

The entire periphery of Curaçao is framed by an uplifted Pleistocene reef; intertidal forms are common all around the coast. But the central areas are underlain by volcanic rocks that erode more easily than the coastal limestone. During the last glacial period, when sea levels were lower, extensive drainage systems were developed on the volcanic terrain; these breached the harder limestone rim in only a few places. These valley systems were drowned when sea level rose and produced the outstanding protected harbors that characterize all three islands: narrow inlets with expansive inland waters. Willemstad, the capital of Curaçao, is built on both sides of the largest harbor, the Schottegat. The inland shores of the Schottegat are volcanic; in the absence of strong surf and a rocky coast, the rock-dwelling intertidal forms do not inhabit these shores. I conclude that the Kintján shells were collected in the Schottegat (Fig. 4b); the extensive, calm, shallow waters provided an excellent site for gathering.

3. Tafelberg

GASTROPODA PROSOBRANCHIA

TROCHIDAE

Cittarium pica — several fragments

LITTORINIDAE

Tectarius muricatus

GASTROPODA PULMONATA

CERIONIDAE

Cerion uva — common, 5 of 111 have intact apices

BIVALVIA

ARCIDAE

Arca imbricata — 1

CHAMIDAE

Chama macerophylla — common

The site has been thoroughly disturbed by blasting.

4. Ceru Canashito

AMPHINEURA

Acanthopleura granulata — 4 plates

GASTROPODA

TROCHIDAE

Cittarium pica — 8

TURBINIDAE

Astraea tecta — 1

NERITIDAE

Nerita tessellata — 3

LITTORINIDAE

Tectarius muricatus — 5

MODULIDAE

Modulus modulus — 1

CERITHIIDAE

Cerithium algicola — 1

Cerithium litteratum — 1

STROMBIDAE

Strombus gigas — common

MURICIDAE

Murex pomum —7

Murex brevifrons — 1

Thais deltoidea — 1

MELONGENIDAE

Melongena melongena — common

XANCIDAE

Vasum muricatum — common

BIVALVIA

ARCIDAE

Anadara notabilis — common

PTERIIDAE

Pinctada radiata — 1

LUCINIDAE

Codakia orbicularis — common

CHAMIDAE

Chama macerophylla — common

Pseudochama radians — 1

Intertidal rock-dwellers are found here, but the series is not nearly so complete as at Rooi Rincón (only one *Nerita, Tectarius,* but neither *Echinus* nor *Nodilittorina*). Among shallow water forms, there are two major differences between Canashito and both Rooi Rincón and Kintján. The Curaçao sites contained a suite of mangrove-dwellers that are completely absent here (Canashito yielded one *Murex brevifrons,* a common mangrove form, but *Murex ponum,* an open water species absent from both Curaçao sites, is the common *Murex* here). In addition, Canashito contains a suite of shells (*Modulus,* the two *Cerithium* species and, especially, the common *Codakia orbicularis*) that inhabit grass and algal beds; none of these occur in the Curaçao deposits. The shells were probably collected in calm waters off the leeward south coast, near the site of the present airport.

CERION UVA IN THE PRECERAMIC MIDDENS OF CURAÇAO

In all three preceramic middens of Curaçao, the most common molluscan shell is that of the land snail *Cerion uva.* These shells present two outstanding features: more than 80 percent in each locality have lost their apical whorls and shells are larger and more variable than modern specimens.

1. *Removal of the apical whorls.* By reason and experiment, one of a list of possible proposals can be identified as the cause of removal. I list the suggestions made to me by many friends and colleagues.

A) Natural removal
B) Artificial removal
   i) by biting
   ii) by rubbing
   iii) by crushing (striking with the shell held upright)
   iv) by slicing (striking with the shell placed on its side).

Although the apical whorls form the weakest part of the shell, I do not believe that they could have been lost naturally by so many specimens. I have extensive collections of much older fossils from fissure-fills on Aruba. These tumbled, often down several meters, into the fissures, suffered strong compaction, underwent tectonic uplift and still retain, in almost all cases, the apical

whorls. I have never seen a natural accumulation, either recent or fossil, in which many specimens are missing their apical whorls.

After suffering one dental misfortune, I am quite sure that the tops cannot be bitten off. Apices can be removed by rubbing either against limestone or volcanic rock, but the process is much too laborious and time-consuming. I am convinced that the tops were removed by striking. They were not crushed by striking the top of the shell while holding the bottom against a substrate (and keeping the shell vertical), for this process invariably breaks the lower lip of the aperture before crushing the top. If, however, the shell is placed on its side, horizontally against the substrate, the top can easily be removed by striking with a sharp instrument. In fact, the flint chips and stone tools of Rooi Rincón and Kintján, are excellent devices for this purpose. With a bit of practice, the apices can be removed with a single blow.

This leaves open the question of why the apices were removed. I can imagine three interpretations:

A) Removal is unrelated to eating; the shells were used for an ornamental or other purpose.

B) When the top is removed, the animal can be sucked out through the apical hole thus produced.

C) Removal of the top aids, somehow, in sucking the animal out through its normal aperture.

I cannot imagine what nongastronomical purpose so many thousand decapitated shells could have served. Moreover, the following demonstration that decapitation is an aid to removal of the animal argues strongly against A.

Figure 5. X-ray photographs of decapitated *Cerion uva* from Kintján (left 2 specimens) and Rooi Rincón (right 2). Since internal whorl partitions are intact, animal was not removed through apical hole. Specimen on left is 32.8 mm high.

If the animal were sucked out through the top, some of the internal whorl partitions would have to be broken, for the large foot could not fit in the small whorls left near the top of the shell. X-ray photographs of decapitated shells (Fig. 5) show clearly that the whorl partitions are never disturbed. The animal could not have been extracted through the apical hole.

If you take an intact shell with its animal inside and suck as hard as possible at the aperture, the animal cannot be extracted. But, when the apex is removed, a single hard suck upon the aperture will extract either the large foot of the animal or the entire body itself. Removal of the top breaks the vacuum inside the shell and facilitates the extraction of its contents. The entire process is really quite efficient: one strike, one suck, and the animal is removed. Several can be eaten in a minute (though I recommend *Cerion* only to the starving).

Somehow, I find it satisfying to think that the Meso-Indians of Curaçao discovered an important physical principle for such a practical procedure. This idea, so obvious to all of us who were raised in the pre pop-top age of the beer can industry, is by no means a self-evident principle.

2. *Variation and form of* Cerion uva. Any sample from a shell midden is, of course, strongly biased from a biometrical point of view. The probable bias, in these cases, is twofold: the selection of large individuals (for *Cerion* is not a large snail and much work must be expended for little nutrition), and the amalgamation of shells from several local populations.

Much has been made in the literature of the extreme intraspecific variability of land snail shells. This indeed is true, but it is usually of a particular kind (and this is rarely emphasized). The variation is interpopulational, i.e., the shells of any local population are not unusually variable, but differences among the means of local populations are often extreme. Thus, it is likely that our two biases will affect the mean of a midden sample in opposite ways: the selection of large shells will augment the mean, but the amalgamation of large individuals from several local populations will produce a midden mean smaller than the true mean of a local population with large shells.

The rise in variability from amalgamation of local populations can be gauged by comparing coefficients of variation (C.V.) (Simpson, Roe, and Lewontin, 1960: 89–95) of midden samples

and modern local populations for the same character. Table 2 presents C.V.'s for shell height of the three midden samples and a mean value for 69 modern local populations (Gould, unpublished data for monograph in preparation; N = 20 for all samples, midden and modern; values for midden shells are estimates for actual height with decapitated apical whorls restored; all shells are adults with completed growth). All midden means are above the modern grand mean. Rooi Rincón and Tafelberg are within the span of modern C.V.'s (4.03 to 10.18), but, at 15.45, shells from Kintján are far more variable than those of any modern local population.

The striking feature of midden samples is the large size of some of their shells. Fortunately, *Cerion uva* is among the world's best known land snails from a biometrical point of view. Three major studies have been done in this century: by Baker in the early 1920's (Baker, 1924), by Hummelinck in the late 1930's (Hummelinck, 1940) and by myself during the past two years. Table 2 compares the heights of shells in midden and modern samples. Each modern study has uncovered a local population with greater mean height than the smallest midden sample, and one of Hummelinck's local populations exceeds the largest midden sample in mean height. Still, of course, the midden means are all well above

Figure 6. Comparison of largest shell heap (left, from Kintján, 34.3 mm high) *Cerion* and largest modern shell. Difference is much more striking in actual shells in which areal artifact of two dimensional representation is lost and judgment of size is made more properly by volume.

the grand mean of means for each modern study. However, as mentioned previously, the midden means are almost surely lower than the true means of local populations with large shells living at that time. A more appropriate comparison might be made using maximal size.

Among almost 12,000 modern snails from 248 local populations over 50 years, no snail greater than 30 mm in height has ever been found. (In only one of Hummelinck's local populations did any individuals exceed 29 mm; neither Baker nor Gould found any taller than 28.5 mm.) Yet snails exceeding 30 mm in height are very common in two of the three midden samples and, at 34.3 mm, the largest snail from Kintján dwarfs my modern "giant" (Fig. 6).

Two separate factors can make a snail tall, and both operated to produce the large midden shells. First, a snail can increase in height simply by adding more whorls. Each of the decapitated shells of Figure 5 shows 11 whorls below the break; the complete shell would have had one or two more postprotoconch whorls. Modern shells with more than 10½ postprotoconch whorls are a great rarity (Baker and Hummelinck included protoconch whorls in their count, hence their larger figures). Secondly, a tall snail may have as many whorls as a smaller one, but simply have larger whorls. Protoconch size is a good measure of general whorl size (Gould, 1969). Only Rooi Rincón has enough complete shells to permit the calculation of mean protoconch width. At 1.67 mm, mean protoconch width for Rooi Rincón is at the top of the range of modern mean widths (1.41–1.69 mm for 69 samples, N = 20 for each sample). The midden shells grew more whorls than any modern sample and had larger whorls than most.

Why were the midden snails larger than modern snails? All three modern studies have demonstrated the extreme phenotypic plasticity of *Cerion uva*. Shell size of adults is a direct function of microenvironment; snails are large when habitats are moist, calm, and well vegetated. Curaçao today is an arid island. It receives only 17–22 inches of rain per year, most in brief downpours. It is hard to imagine a less hospitable area in the West Indies for pre-agricultural Meso-Indians. I do not know what they could have found, in this cactus-covered land, to supplement a diet of sea food. It is therefore tempting to think that the large midden shells indicate a wetter climate that might have supplied to Meso-Indians some of the tropical fruits that adorn most West Indian

islands. Unfortunately, there is no other evidence for greater rainfall 4000 years ago. If Curaçao were much larger or higher than it is today, continental effects might lead to increased rainfall. But the eustatic rise of sea level has not been more than 10 feet during the past 4000 years (Redfield, 1967; Milliman and Emery, 1968) and the direction of tectonic movement has been upward (Weyl, 1966). Rouse and Cruxent (1936: 38) believe that temperatures and rainfall have not varied appreciably during the past 5000 years in Venezuela and surrounding areas.

If large size is not an immediate phenotypic response to local conditions more favorable than today's, then I suspect that the midden snails were programmed to be large, i.e., that the effect is mainly genetic. In this case they probably represent the relict populations of snails that had been genetically adapted to more favorable conditions during pluvial cycles of the previous glacial period. In any event, they served the Meso-Indians well; it would be hard to make a meal of modern *Cerion*.

There is an interesting postscript to the relationship of *Cerion* with Meso-Indians. There is considerable evidence for trade between the mainland and coastal islands, but it is all unidirectional. Rouse and Cruxent (1963: 45) found trade pottery from Venezuela in the Punta Gorda complex of the Manicuaroid Series on Cubagua. Du Ry (1960: 85) discovered that the oldest pottery of Aruba is finer in texture than later examples. He assumes that this first pottery was imported from northeastern Venezuela and that the later work is indigenous. In a nearly-forgotten work, Berry (1934) found *Cerion uva* in an Indian shell heap near Lake Valencia, Venezuela. Berry was not convinced that these shells were imported from the Dutch Leeward Islands. But his argument that *Cerion* might have once inhabited the shores of Lake Valencia can be discounted because this halophile would not survive so far inland. I also doubt that *Cerion* inhabited the coast of Venezuela, for it has never been recorded from shell heaps there. Since there is no evidence that *Cerion uva* ever lived elsewhere than the Dutch West Indies, I conclude that the Valencia specimens establish the reciprocity of transport between Venezuela and the islands.

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TABLE 1

Age of Shell Middens on Curaçao and Aruba

	Charcoal	Chama	Cittarium	Anadara	*Period*	*Island*
Rooi Rincón	3990±50-4490±60 (range of 5 dates)	4090±125	4705±160		Meso-Indian	Curaçao
Kintján		4150±140	3530±140		Meso-Indian	Curaçao
Tafelberg		3830±140	3665±140		Meso-Indian	Curaçao
Ceru Canashito		1685±115	815±105	1345±120	Neo-Indian	Aruba

TABLE 2

Size and Variability of *Cerion uva* in Indian Shell Middens and Modern Populations; in mm.

Sample or Study	*Height of Largest Specimen*	*Mean of Height*	*Largest Mean for Height*	*Smallest Mean for Height*	*C.V. for Height*	*Number of Specimens*	*Number of Samples*
Kintján	34.3	25.99			15.45	347	1
Rooi Rincón	31.7	26.30			8.74	129	1
Tafelberg	29.0	24.59			7.39	111	1
Baker, 1924	27.8		25.1	19.6		2,737	44
Hummelinck, 1940	29.5		26.4	19.4		6,540	66
Gould, unpublished	28.4		24.68	16.43	6.27*	2,622	138

* Mean value for 69 samples.

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA.

VIII. A FRAGMENTARY SKULL OF A LARGE THECODONT, *LUPEROSUCHUS FRACTUS*

Alfred Sherwood Romer

ABSTRACT. Incomplete remains of a large skull, not improbably representing a rauisuchid thecodont from the early Middle Triassic of Argentina, are described as *Luperosuchus fractus*, gen. et sp. nov. Large dermal scutes, found isolated, may pertain to this form.

INTRODUCTION

A moderate number of specimens assignable to the reptilian order Thecodontia are present in our Chañares collections. Apart from materials that are difficult of interpretation or assignment, there are definitely present: (1) a small and primitive member of the Ornithosuchidae; (2, 3) two long-snouted forms, with general proportions resembling crocodilians, but without any positive indications of affinities with that group; (4) a small form with a very lightly built skull, of which the limbs are unknown; (5, 6) two forms known from very slender hind limbs of unusual construction; and (7) a large animal, probably a rauisuchid, represented only by a partial skull. In addition there are various isolated materials, pseudosuchian in nature. In the present short paper I shall describe only the last specimen listed, leaving the others for later description.

Since our collections were made, Sr. Bonaparte of Tucuman has made several visits to the Chañares region, and found, *inter alia*, a fair amount of thecodont material. He invited me to make use of this in my work on thecodonts, and in June 1970 I spent a week in Tucuman studying this material. I found no identifiable forms not already present in the Harvard-La Plata collections,

but in a number of regards his materials supplemented ours and substantiated our conclusions. I am deeply grateful to Sr. Bonaparte and the authorities of the Instituto Lillo for placing this material at my disposal.

Luperosuchus fractus gen. et sp. nov.

Combined generic and specific diagnosis. A large thecodont, with an estimated skull length of about 60 cm, probably pertainable to the family Rauisuchidae. A slitlike opening apparently present posterior to the nares between premaxilla and maxilla; antorbital opening large; apparently no parietal foramen; lateral temporal opening with vertical posterior border; archosaur type of otic notch partially developed.

Holotype of the species. La Plata Museum 1964–XI–14–9, an incomplete skull, consisting of most of the dermal roof and part of the left side of the "face" collected from the Chañares Formation in La Rioja Province, Argentina, north of the north fork of the Chañares River, about 5 km NE of the point where this river emerges into the Plano de Talampaya.

The generic and specific names refer to the fragmentary and perplexing nature of the type material.

I am indebted to National Science Foundation Grant GB–2454 for aid in the collecting of the material and to further grants for its preparation and for publication costs.

Figure 1. Side view of the fragmentary type skull of *Luperosuchus fractus*, as preserved. × 1/6.

Description. This form is represented by a single fragmentary specimen that includes most of the dorsal surface of a skull and part of the dermal bones of the left side of the skull (Figs. 1, 2). The condition of the material is none too good, and sutures are generally difficult to determine. The specimen was found close beside the skeleton of a dicynodont. Near it were found a considerable number of weathered scraps of bone; whether they belong to the specimen here described or to the dicynodont is uncertain.

The animal was a large one; the portions of the skull preserved measure 54.5 cm in length and if the missing anterior and posterior regions be restored, the length in life would have been about 60 cm. In general, the reptiles present in the Chañares Formation are of modest size; apart from this *Luperosuchus* specimen, the dicynodonts are the only large animals known.

As mentioned, most of the skull roof is preserved; the cranium was obviously long and slender, as in many early archosaurs. Posteriorly, the parietals are incomplete, and their posterior extensions, which presumably formed the median boundaries of the superior temporal fenestrae, are missing. There was no parietal foramen in the portion of the bone preserved (although it may possibly have been present in the missing posterior portion). A median longitudinal suture can be made out for almost the entire length of the roof as preserved. Other sutures are obscured by poor preservation and bone fusion in this seemingly mature skull.

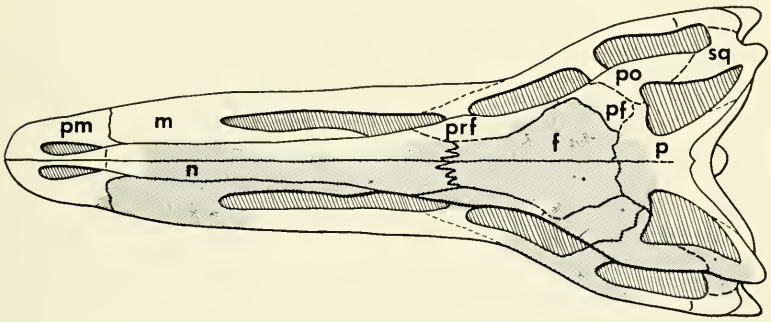

Figure 2. Dorsal view of the skull, restored. Parts present in stipple. Abbreviations: *f*, frontal; *j*, jugal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *p*, parietal; *pf*, postfrontal; *pm*, premaxilla; *po*, postorbital; *prf*, prefrontal; *qj*, quadratojugal; *sq*, squamosal. × 1/6.

I have restored the probable sutural pattern, but it should be emphasized that uncertainties exist.

The area of the posterior part of the frontals and the median portion of the parietals is depressed, and bounded on either side by prominent ridges running back along the lateral margins of the frontals and continuing backward along the parietals. Postorbitals are present along the back portion of the supraorbital rims and extend backward and medially to meet the parietals along the anterior border of the superior temporal fenestrae. As far as can be determined, there were large postfrontals, forming part of the upper margins of the orbits and extending back between frontals and postorbitals to gain contact with the parietals. The frontals are broad posteriorly; anteriorly they become reduced in width between the prefrontals. It is possible that the frontals entered the orbital margins briefly, but imperfections of the specimen render this uncertain, and they may have been excluded by a narrow contact between postfrontals and prefrontals. The latter elements appear to be relatively narrow, projecting somewhat outward over the anterodorsal corner of the orbits and extending a modest distance forward on either side on the dorsal surface. Anteriorly, about opposite the front margin of the antorbital vacuity, the nasals, as seen in side view, rise upward markedly above the general line of the skull roof on their forward course. I was at first inclined to believe this appearance was due to post-mortem distortion; however, inspection indicates that this "roman nosed" effect is a real structural feature; the conjoined nasals form a sharp ridge below which the two bones are apposed for some distance and then slant outward toward either side ventrally. It seems obvious that the nasals are incomplete anteriorly. Ventrally the point of separation of the nasal from the posterior extension of the premaxilla below it indicates the probable position of the posterior angle of the naris. Most of the premaxilla is missing. A small fragment of bone attached to the anterior end of the maxilla presumably represents the most posteroventral position of the bone. More dorsally a band of bone with well-defined margins extends dorsoposteriorly between maxilla and nasal, indicating a posterior extension of the premaxilla that excludes the maxilla from the narial margin, as in certain other thecodonts (and ornithischians). The whole aspect of the anterior portion of the skull, as far as preserved, strongly suggests the presence

of an expanded narial area, and in Figure 3 I have restored the narial region on this supposition.

A large portion of the maxilla is present. A ventroanterior area, much thickened, represents the ventral margin adjacent to the premaxilla. This region is excavated internally and, although preservation is imperfect, represents the area of insertion of a series of large, probably subthecodont, anterior maxillary teeth. Above this region the anterior margin of the maxilla slants upward and backward parallel to the posterodorsal extension of the premaxilla. In the specimen as preserved the two bones are separated here by a long if narrow slit. For much of this distance the facing margins of both bones are broadened so that they can readily be apposed to one another; hence, when I first attempted a restoration of the skull, I placed these margins in firm apposition. But in contrast to the close union of all other portions of the skull, in the specimen as preserved, there was here a very distinct separation, suggesting that a slitlike opening was present in life. Dr. W. D. Sill, who is currently studying *Saurosuchus,* a seemingly related form from the Ischigualasto Formation, informs me that such an opening was definitely present in that genus, and I have therefore indicated such an opening in the restoration in Figure 3. I have no worthwhile suggestion as to the possible function of this slit.

Back of the nasal region, dorsal and lateral surfaces are sharply separated for most of the skull length and, even allowing for possible crushing, it seems certain that the side walls descended nearly vertically from the lateral dorsal ridges. A short length of maxilla is preserved ventrally; above, there is a broad plate of bone apparently formed by the maxilla, extending back above the antorbital fenestra. The margins of this fenestra are, for the most part, clearly outlined; it was an opening of considerable size. In many advanced thecodonts the fenestra is centrally situated in a depressed area of the cheek; in this specimen the anterior rim of this depression is clearly incised in the maxilla. The suture between prefrontal and lacrimal is not clear, but the latter bone apparently includes the posterior part of the upper margin of the antorbital fenestra as well as the preserved portion of a stout bar of bone that separates orbit and antorbital fenestra. Behind the orbit, the bar of bone between orbit and lateral temporal fenestra is completely preserved, and there are indications of a suture well

down this bar, between postorbital and jugal. A fraction of the latter bone is present, defining the lower margin of the orbit, a section of the cheek rim, and a small area of the anteroventral margin of the lateral temporal fenestra. Above this fenestra a stout bar of bone is present, presumably formed anteriorly by the postorbital, posteriorly by the squamosal (the suture between the two is not clear). An incomplete flange of the latter bone extends directly downward as part of the posterior border of the lateral fenestra. The squamosal extended backward beyond the level of this descending flange, although this extension is broken off in the specimen. The vertical descent of the squamosal flange indicates that the posterior border of the fenestra had not acquired the V-shaped contour seen in various more advanced thecodonts; on the other hand, the posterior prong of the squamosal suggests the initiation of a typical archosaur type of otic notch.

In Figure 3 I have freely restored the skull in side view to give a suggestion of its probable appearance in life. Despite the incomplete nature of the evidence I do not think that there can be too great a departure from life conditions in most regards. Most doubtful, because of lack of material, is the suspensorial region.

Systematic position. As to relationships of *Luperosuchus,* an early Middle Triassic form, one tends to think first of the larger erythrosuchid members of the Proterosuchia — a group most recently discussed by Reig (1970), and by Charig and Reig (1970). Primitive, for example, is the apparent presence of a large postfrontal. *Luperosuchus,* however, is more advanced than

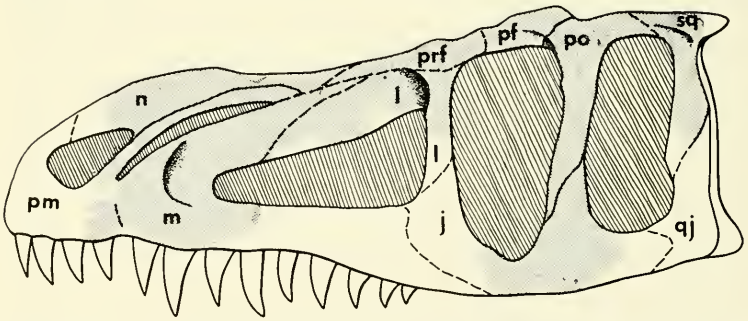

Figure 3. Side view of the skull, restored. Abbreviations as in Fig. 2. × 1/6.

proterosuchians in various regards, such as the large size and incised nature of the antorbital fenestra, probable absence of a parietal foramen, and the apparent beginning of the pseudosuchian development of an otic notch. More reasonable is assignment to the Rauisuchidae (or Prestosuchidae), a family of large but relatively primitive Middle Triassic thecodonts, first seriously studied by Reig (1961). Included here may be such forms as *Ticinosuchus* from the European Anisian (Krebs, 1965), *Fenhosuchus* and, doubtfully, *Shansisuchus* from China (Young, 1964), *Stagonosuchus* (Huene, 1938), and *Mandasuchus* from the Manda beds of East Africa. The presence of rauisuchids in the Middle Triassic of South America is well attested by the presence of *Rauisuchus* and *Prestosuchus* from the Santa Maria of Brasil and *Saurosuchus* of the Middle Triassic Ischigualasto Formation of Argentina.

The material of *Luperosuchus* is too fragmentary to warrant any extended discussion of rauisuchid relationships. Are they, as Reig believes (1970, fig. 10), a side branch from a somewhat advanced pseudosuchian stock, or could they have progressed in parallel fashion from the proterosuchian base of the Thecodontia? Are they a sterile group, without descendants, or could they be related to the ancestry of certain of the later saurischians, the Prosauropoda (Palaeopoda) or, more especially, ancestral Sauropoda? It is possible that Dr. Sill's current studies of *Saurosuchus* will shed light on rauisuchid relationships.

Dermal scutes. In two instances we found in the Chañares region large scutes not definitely associated with other identifiable skeletal remains (Fig. 4). They are too large to be attributed to any of the other (and much smaller) thecodonts present in our

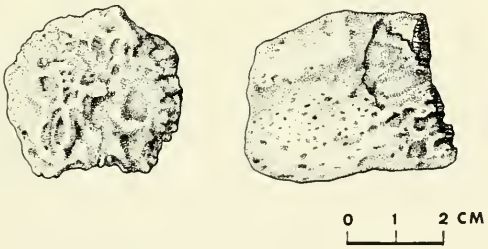

Figure 4. Two dermal scutes, possibly referable to *Luperosuchus*.

collections (and they are not, of course, attributable to the synapsids, which make up the remainder of the materials collected). Of known forms from the Chañares, *Luperosuchus* is the only one to which they could have belonged and, since comparable scutes are known in other rauisuchids, we may provisionally assign them to the present genus. None of the scutes is perfectly preserved. One type, rectangular in shape, has a thickened, saw-toothed border along one edge, indicative of an interdigitating connection with another element. Such scutes are presumably paramedian paired scutes, found in various other thecodonts. Subcircular scutes, also present, may be more lateral elements or median caudal ones.

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BREVIORA

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THE FISHES OF THE MALAYSIAN FAMILY PHALLOSTETHIDAE (ATHERINIFORMES)

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ABSTRACT. The tiny fishes of the family Phallostethidae, from Malaya and Thailand, develop a large penis and differ radically in structure of the bilaterally asymmetrical priapium from the somewhat larger fishes of the more widely distributed Neostethidae, the only other family in the suborder Phallostethoidea. A morphological characterization of the Phallostethidae is given and its features compared to those of Neostethidae. There are three species: *Phallostethus dunckeri* Regan (1913), known only from the type specimens collected in the mouth of the Muar River in Johore, Malaya; *Phenacostethus smithi* Myers (1928), known from the types and many other specimens collected in the khlongs of Bangkok and reported in this paper from Chantaburi Province in southeast Thailand; and *Phenacostethus posthon,* new species, from the Indian Ocean coast of peninsular Thailand. *Ph. posthon* and *Ph. smithi* differ considerably in morphology of the priapium and penis. Furthermore, the asymmetrical priapium in *Ph. posthon* is invariably sinistral. In all other phallostethoids, so far as known, it may be either sinistral or dextral; in *Ph. smithi* the ratio of sinistral and dextral males is near equality (Hubbs and Hubbs, 1945).

The ecology of phallostethids is described for the first time, excepting some brief remarks by H. M. Smith (1927; 1945), who seems to have confused *Phenacostethus* in the field with neostethids and perhaps with *Oryzias.* An hypothesis is offered that the selective advantage of internal fertilization in Phallostethoidea (an oviparous group) lies in permitting temporal separation of mating and spawning activities, corresponding, respectively, with periods of low water and high water in habitats subject to strong tidal fluctuations. Two trends in the reproductive biology of atheriniform fishes that might be conducive to the evolution of internal fertilization are: 1) towards eggs in which either embryonic development is slowed down or temporarily arrested, or hatching of embryos is deferred; and 2) away from expelling all ovulated eggs at once and towards expelling them in small batches or even singly.

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For translations of the papers by Aurich and Woltereck I am obliged to Miss Deborah White and Dr. Elizabeth Deichmann. Prof. George S. Myers read the paper in manuscript.

INTRODUCTION

This account of the family Phallostethidae is the first paper dealing with the fresh- and brackish-water fishes collected by me in Thailand from April 15 to July 14, 1970, and deposited in the fish collection of the Museum of Comparative Zoology. Collecting phallostethoid fishes was one of the main objectives of my fieldwork in Thailand. In addition to *Phenacostethus smithi* Myers (1928) and the new phallostethid described in this paper, large series of the neostethids *Neostethus siamensis* Myers (1937) and *Ceratostethus bicornis* (Regan, 1916) were obtained. These represent the first specimens of *Ceratostethus* recorded from Thailand, and the only specimens of *Neostethus siamensis* other than

the female holotype. (*N. siamensis* is close to, and perhaps specifically identical with, *N. lankesteri* Regan (1916), the type locality of which is the mouth of the Muar River, Johore, and Singapore.) The osteology and functional anatomy of *Ceratostethus* will be considered in another paper.

The Phallostethoidea are small, highly specialized fresh- or brackish-water fishes in which males have a remarkable subcephalic copulatory organ, the priapium. The skeleton and musculature of this complicated bilaterally asymmetrical organ, which functions both in clasping and intromission, are derived mainly from the pelvic fins and girdle. Minor contributions come from the first pair of ribs and anteroventral part of the pectoral girdle. In females the pelvic fins are absent or vestigial. Aurich (1937) divided the Phallostethoidea into two "Familien," but gave these divisions names in subfamily form, Phallostethinae and Neostethinae. Berg (1940: 465–466) recognized them as families, Phallostethidae and Neostethidae, as did Rosen (1964: 261) and Greenwood et al. (1966: 398). Neostethidae, comprising eight genera and about 15 species, have been recorded from Thailand, Malaya, Sumatra, Borneo, and the Philippine Islands. Six of the genera — *Gulaphallus* Herre (1925), *Mirophallus* Herre (1926), *Plectrostethus* Myers (1935), *Solenophallus* Aurich (1937), *Ctenophallus* Herre (1939), and *Manacopus* Herre (1940) — are known only from the Philippines.

The Phallostethidae, even more specialized (and rarer in museum collections) than Neostethidae, comprise three species from the Malay Peninsula and adjacent parts of Thailand. *Phallostethus dunckeri* Regan (1913), the first phallostethoid to be described, is known only from the type specimens Duncker collected previous to 1904 at the mouth of the Muar River, about 20 miles south of Malacca, Johore Province, Malaya (Duncker, 1904: 171). *Phenacostethus smithi,* hitherto known only from several large series collected by H. M. Smith from khlongs in Bangkok, was obtained by me at Bangkhen (a suburb of Bangkok) and at Chantaburi, near the southeast corner of Thailand (near Cambodia). The third species, described in this paper, is from the Indian Ocean coast of Thailand. All localities where phallostethids have been collected are shown in Figure 1. The present paper presents characterizations of the family Phallostethidae and of the phallostethid species, a description of the new species just mentioned, and observations on the ecology of Phallostethidae.

Figure 1. All localities where Phallostethidae have been collected. 1. Mouth of Muar River at Bandar Maharani (type locality of *Phallostethus dunckeri* Regan, 1913); 2. Bangkok (type locality of *Phenacostethus smithi* Myers, 1928); 3. Bangkhen, a suburb of Bangkok (*Ph. smithi*); 4. Chantaburi City (*Ph. smithi*); 5. Khlong La Ngoo, 48 km NW of Satul Town, 6° 52′ 30″ N, 99° 48′ 10″ E (type locality of *Phenacostethus posthon* n. sp.); 6. Khlong Kla Sohm, 15 km S of Pungah Town, on Pakasem Road from Pungah going towards Phuket Island (type locality of *Ph. posthon* n. sp.)

Definition of the suborder Phallostethoidea and discussion of phyletic trends in the Phallostethoidea will be presented in a forthcoming paper on *Ceratostethus*.

Ph. smithi provides an Asian example of the phenomenon (of which Africa and South America provide numerous examples)

that the smallest fishes amidst the richest tropical freshwater faunas are representatives not of the dominant fish groups present, but of groups with a marginal distribution pattern. The ecology of such minute fishes, when known, usually proves to be highly specialized.

Rosen (1964) united the exocoetoids, scomberesocoids, adrianichthyoids, cyprinodontoids, atherinoids and phallostethoids in a new order, the Atheriniformes. Atherinoids and cyprinodontoids were widely separated in earlier classifications, the artificiality of which has become increasingly apparent. Such similarities as were noted between atherinoids and cyprinodontoids had usually been attributed to convergence. Having personally investigated the osteology of phallostethoids (which evidently are related to atherinoids), atherinoids, and cyprinodontoids, and reviewed much of the literature on osteology and reproductive biology of these groups, I am inclined to believe that they may be related. Some of the similarities in reproductive biology were first brought to my attention in a talk given by Neal R. Foster at the 1968 meetings of the American Society of Ichthyologists and Herpetologists.

Note on the figures. Figures 2–5, prepared with the aid of a Wild microscope and camera lucida, are based on formalin specimens. Formalin specimens of Phallostethidae are more nearly normal in appearance than alcoholic specimens, since the latter invariably undergo at least some shrinkage. In specimens that have been transferred from the original formalin fixative to 60 per cent ethyl alcohol for permanent storage, teeth protrude more from the gums, scales stand out more clearly, the membranous dome atop the head has disappeared, and the caudal peduncle is decidedly narrower.

CHARACTERIZATION OF THE FAMILY PHALLOSTETHIDAE

The following characterization of the Phallostethidae is based on my observations of *Ph. smithi* and *Ph. posthon,* including study of alizarin preparations, and on accounts of *Ph. smithi* by Myers (1928), Bailey (1936), and TeWinkel (1939), and of *Phallostethus dunckeri* by Regan (1913; 1916).

1. Slender elongate phallostethoids, very delicate, largely translucent, with deciduous scales; externally visible concentrations of melanophores restricted to the top of the braincase, middle of the

dorsum, midlateral intermuscular septum, priapium, and bases and edges of fin rays; maximum standard length about 23 or 24 mm.

2. Dorsum of head with a translucent, membranous dome.

3. Mature individuals of both sexes with a bright orange-yellow bar on caudal peduncle.

4. Branchiostegal rays 4.

5. Main "externalized" clasping bone in the priapium is the toxactinium; ctenactinium reduced or absent.

6. A greatly enlarged, oval, concave pad, or pulvinulus, slightly posterior to toxactinium.

7. Vas deferens terminating in a large penis that projects considerably from the priapium.

8. Pelvic spines or rays, if present, greatly reduced and modified beyond recognition.

9. Vas deferens highly coiled, forming a sort of epididymis.

Comments on the family characters. Neostethids, while small as fishes go, are all or almost all larger when adult than phallostethids. Most, if not all, neostethids are hardier fishes than phallostethids and have relatively adherent scales. While they also are largely translucent, neostethids usually have relatively more melanophores than phallostethids. The epidermis paralleling the scale margins is often well provided with melanophores in neostethids but invariably devoid of melanophores in phallostethids. Neostethids (*Ceratostethus* and *Neostethus*), even at comparable sizes, lack a membranous dome on the dorsum of the head, or if one is present, it is not notably elevated. According to TeWinkel (1939) this region bears sensory canals in both *Phenacostethus* and *Gulaphallus*. In neostethids large sensory pores are evident in the frontal region, whereas the membranous dome in phallostethids is apparently entire.

With regard to characteristic number 3 (bright orange-yellow markings at the base of the caudal fin and sometimes at the origin of the anal fin), these are present in living specimens of *Ph. smithi* and in *Ph. posthon*. There is no way of telling whether such spots are also present in *Phallostethus*. The orangish yellow coloration, contained in chromatophores (approximately 50–75 chromatophores constituting the caudal base mark) gradually disappeared after a few weeks of preservation in formalin. Similar markings

were definitely absent in live specimens of *Neostethus* and *Ceratostethus* observed by me, nor is there any mention of such marks in the literature on Neostethidae.

Concerning character 4, Neostethidae usually have 5 branchiostegal rays. The number of branchiostegal rays in *Phallostethus* is unknown.

Characters 5–9 concern the priapium, which differs fundamentally from that of Neostethidae. In Neostethidae the main "externalized" bony clasping element, the ctenactinium, is apparently a modified pelvic fin ray or spine. The main "externalized" bony element in the priapium of phallostethids, the toxactinium, is not homologous with the ctenactinium. My observations confirm Bailey's view (Bailey, 1936: 463, 471) that it is homologous with the pulvinular bone, one of the anteriormost internal bony elements in the priapium of neostethids. The homologies of this element are unclear, but it is almost certainly not a modified pelvic ray or spine. The ctenactinia of phallostethids, which may or may not be homologous with the elements called ctenactinia in neostethids, are greatly reduced in size. The ctenactinium of *Phallostethus dunckeri,* while relatively short, bears several "teeth" or sharp projections; these are perhaps comparable to the single curved hook present near the base of the ctenactinium in *Neostethus*. The pulvinulus of phallostethids probably functions as a pad in conjunction with the toxactinium. A homologous but much smaller pulvinulus is present in neostethids. A striking characteristic of the phallostethid priapium is the development of a large penis. In *Phenacostethus posthon* the organ is entirely smooth; in *Ph. smithi* its distal half bears a series of stiff ruffled pleats. The development of a large penis evidently occurred independently in the neostethid *Mirophallus bikolanus* (Herre, 1926, pl. 3, fig. 1). In most neostethids a complicated flap covers the opening of the vas deferens (Aurich, 1937). This flap is absent in Phallostethidae. Various bony elements in the priapium of phallostethids, including a peculiar slender element lodged in the concave side of the penis bone in *Ph. smithi,* may be homologous with pelvic rays, but the priapium of phallostethids does not bear any branched elements that obviously are relatively unmodified pelvic rays. Several branched pelvic rays of relatively normal appearance occur in the neostethids *Ceratostethus, Neostethus, Solenophallus,* and *Gulaphallus* (personal observations; Aurich [1937], TeWinkel [1939], Woltereck [1942 a, b]).

The priapium of *Phallostethus* is clearly of the same general type as that of *Ph. smithi* and *Ph. posthon.* In *Phallostethus* the toxactinium and pulvinulus are very similar to these structures in *Phenacostethus.* It is likely that *Phallostethus* develops a large penis. The penis in phallostethids, like the ctenactinium of neostethids, only reaches its full development in the largest males.

Regan (1916: 22) hypothesized that in *Phallostethus* the toxactinium grips the female under the chin or is held in her mouth, while the serrated edge of the ctenactinium gives a firm hold on the pectoral region in front of and on the far side of the genital orifice, in order that the seminal papilla could be placed against it or introduced into it. In *Neostethus* he hypothesized that the female is held across the back of the head by the ctenactinium, the anterior descending part of which lies on the side of the female away from the male. Copulation has yet to be observed in *Neostethus* or in any phallostethids. It has been observed only in the neostethid *Gulaphallus mirabilis.* In this species the female is held across the back of the head by the ctenactinium; the "second ctenactinium" of *Gulaphallus mirabilis,* which actually is an externalized pelvic bone, apparently rests or presses against the female's opercular region on the side next to the male (Villadolid and Manacop, 1934: pl. 5, fig. 2). The reduced ctenactinium of Phallostethidae could hardly function in the same manner as the elongate ctenactinium characteristic of all neostethids. It may be that the toxactinium is held, not under the female's chin or in her mouth, but atop the front of her head.

In *Phallostethus* (Regan, 1916: 19, fig. 14) the vas deferens is highly coiled within the abdominal cavity to form a sort of epididymis. TeWinkel (1939) reports a similar coiling of the vas deferens in *Ph. smithi.* In *Neostethus lankesteri* (Regan, 1916: 10, fig. 6) and in *Gulaphallus mirabilis* (Villadolid and Manacop, 1934: pl. 3, fig. 4) the vas deferens is unconvoluted from its origin on the testis to where it enters the priapium, then forms an expanded loop inside the priapium. The sperm of *Neostethus lankesteri* (Regan, 1916: 13, fig. 9) are concentrated into "spermatophores," more properly called spermozeugmata (Nielsen et al., 1968: 248). Regan (1916: 19) stated that *Phallostethus* evidently did not produce "spermatophores" like those of *Neostethus.* In mature *Neostethus* and *Ceratostethus* (personal observation) the posteriormost portion of the priapium is

sometimes greatly swollen with closely packed, adherent small vesicles that presumably are spermozeugmata. The priapium apparently does not become similarly swollen in phallostethids.

Insofar as can be determined from examination of the bones only, the contributions of the first pair of ribs and of the shoulder girdle to the priapium is the same in Phallostethidae and Neostethidae.

THE SPECIES OF PHALLOSTETHIDAE

Phallostethus dunckeri Regan 1913

Phallostethus dunckeri Regan, 1913: 550, figs. 1–4 (original description; types from mouth of Muar River at Bandar Maharani, Johore, Malaya; soft anatomy). — Regan, 1916 (soft anatomy, histology, osteology, comparison with *Neostethus*).

This species is known only from the specimens collected by G. Duncker at the mouth of the Muar River at Bandar Maharani, Johore, Malaya. The following statements are based on the two accounts of this species by Regan (1913, 1916). It is characterized by an exceptionally long anal fin, with 26–28 elements (eight to ten rays more than are found in phallostethoids with the next highest number of anal fin elements), an anal base about 30 per cent of the standard length (compared to anal base 20–25 per cent of standard length in all other phallostethoids) and origin of anal considerably nearer to snout tip than to end of hypural fan (anal origin slightly to considerably nearer to end of hypural fan than to snout tip in all other phallostethoids), and by a serrated ctenactinium (Regan, 1916: fig. 13). Regan did not have very many specimens (some were used for histological preparations or cleared in oil of cloves for bone study). Dr. P. H. Greenwood informs me that the British Museum (Natural History) has four specimens (types?) of *Phallostethus dunckeri* in rather poor condition. Although Regan's specimens of *Phallostethus dunckeri* (at 23–29 mm in total length) are larger than *Phenacostethus,* and the males figured by him have well-developed priapia, perhaps the penis is not fully developed in them. This seems likely, because in both species of *Phenacostethus* the largest females are only about one-half to one millimeter longer than the largest males, whereas Regan's largest female of *Phallostethus* is six millimeters longer than his largest male. In *Phenacostethus* the penis is fully formed only in the largest males.

The second dorsal fin of *P. dunckeri* has eight to ten elements (a number found in some Neostethidae); the highest number in *Phenacostethus* is seven. It is unknown whether *Phallostethus* has a first dorsal fin. Regan did not mention its presence, but he overlooked the first dorsal in his material of *Neostethus lankesteri* and *Ceratostethus bicornis*. *Phallostethus* probably has a small spinous first dorsal fin, but the absence of one would not be unique among Phallostethoidea: the first dorsal is lacking in the neostethids *Mirophallus bikolanus* Herre (1926), (Herre, 1942: 141; Myers, 1937: 142) and *Solenophallus thessa* Aurich (1937: 265).

Phenacostethus smithi Myers 1928
(Figures 2, 4, 6)

Neostethus lankesteri (not of Regan) Smith, 1927: 353–355 (misidentification).

Phenacostethus smithi Myers, 1928: 6, figs. 1 and 2 (original description; types from Bangkok; holotype in American Museum of Natural History). — Bailey, 1936 (osteology). — TeWinkel, 1939 (soft anatomy). — Smith, 1945: 475 (Bangkok; synonymizes *Ph. thai* Fowler; ecology).

Phenacostethus thai Fowler, 1937: 219; figs. 189, 190 (original description; Bangkok; holotype in Philadelphia Academy).

Material studied. MCZ 47055, 13 specimens, five females 13.7–14.8 mm and eight males 13.6–14.9 mm (three with toxactinium arising on left side, five on right side), from Khlong Bangkhen at bridge on Nzarm Wong Wan Road, a few km west of Kasetsart University, Bangkhen, Bangkok, Thailand, 30 April 1970; MCZ 47299, 20 specimens, three females 13.4–15.6 mm and 17 males 12.7–14.9 mm (12 with toxactinium arising on right side, five on left side), from Khlong Kee Nawn, behind Catholic church in Chantaburi City, Chantaburi Province, Thailand, 5 May 1970.

Myers' figure 1 of *Ph. smithi* does not show the membranous dome of the dorsum of the head (Fig. 2); it is likely to be shrunken in alcoholic specimens. The adult male in Myers' figures 1 and 2, at 13.5 mm in standard length, does not have the penis as fully developed as in my specimens 14.3 (Fig. 2), 14.1 (Fig. 4), and 14.5 (Fig. 6) mm in standard length. In these specimens the penis is much larger, and its distal end bears a series of a half-dozen or more crenulated radial folds or extensions resembling a

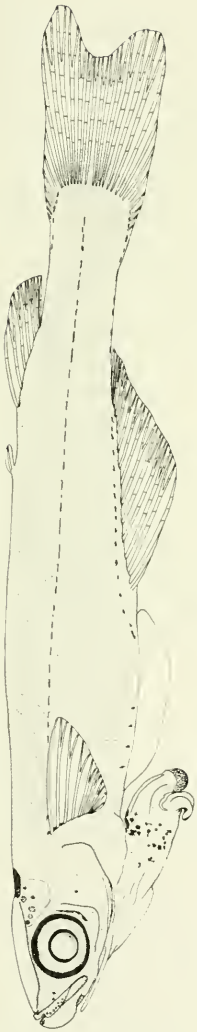

Figure 2. *Phenacostethus smithi* Myers (1928), 14.3-mm sinistral male, MCZ 47299 (formalin).

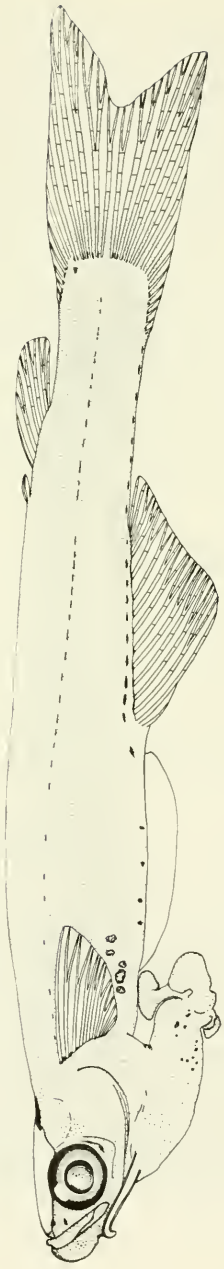

Figure 3. *Phenacostethus posthon* n. sp., 17.3-mm male paratype, MCZ 47301 (formalin).

set of ruffled lace cuffs (best shown in Fig. 4). These folds can be seen in one of Bailey's anatomical figures based on material of *Ph. smithi* collected by Hugh M. Smith. Direct comparison of *Ph. smithi* collected by Smith in Bangkok (deposited in the fish collection of the College of Fisheries, Kasetsart University, and in the MCZ fish collections) with my material from Bangkhen and Chantaburi indicates that only one species is involved. Live specimens of *Ph. smithi* of both sexes from Bangkhen and from Chantaburi had a bright orange-yellow, anteroventrally-posterodorsally oriented bar on the lower half of the caudal peduncle. This bar disappeared from specimens kept a few weeks in formalin. The color was due to about 50–75 chromatophores. There is a small, shiny blue spot over the brain (well behind the eyes), and a very small silvery spot in the middle of the eyes' dorsal surface.

Alizarin preparations reveal the first dorsal fin consists of a single tiny spine, as indicated by Myers. Most specimens are missing many scales. Head scaleless. Abdominal keel scaleless in both sexes (abdominal keel scaled in females of *Ceratostethus bicornis*). Scales on body cycloid, number of scale rows corresponding closely with the number of myotomes. Teeth in both jaws in a single series; medial portion of premaxillary with about eight sharp conical teeth, lateral (expanded) margin of premaxillary with about seven to nine slightly larger conical teeth; medial portion of dentary with about a dozen conical teeth opposing but much smaller than those on medial portion of premaxillary.

For counts of fin elements and vertebrae based on alizarin preparation see Table 1.

Phenacostethus posthon, new species
(Figures 3, 5, 7)

Holotype. MCZ 47300, a 16.7-mm male from Khlong Kla Sohm about 15 km southwest of Pungah Town, where it is crossed by a bridge on the Pakasem Road (between Pungah Town and Phuket), Pungah, Thailand. 29 June 1970.

Paratypes. MCZ 47301, 58 specimens, comprising two immatures, 11.9 and 12.0 mm, 22 females, 12.3–17.7 mm, and 34 males 12.7–17.0 mm (of which two males, 15.5 and 16.5 mm, are cleared and stained), same data as holotype; MCZ 47302, 20 specimens, comprising three immatures 9.6–12.0 mm, 10 females 12.7–18.0 mm, and 7 males 12.9–16.7 mm, from Khlong Langu

at Langu Town, 48 km northwest of Satul Town(6° 52′ 30″ N, 99° 48′ 10″ E). 23 June 1970.

The most obvious differences between this species, from the Indian Ocean coast of Thailand (Fig. 1), and *Ph. smithi* involve the priapium and the position of the dorsal fin. Granted that both species have the characteristic priapial elements of the family Phallostethidae, the priapium is, in fact, so different in the two species that the question may even be raised as to whether separate generic status is indicated.

Differences in the priapium of the two species involve external morphology of the penis, skeleton of the penis, ctenactinium, toxactinium, and the nature of the laterality of the priapium itself. In *Ph. smithi* 1) the distal portion of the penis is ruffled (see description above); 2) the penial skeleton includes a large papillary bone with a slender penial bone lodged in its concave surface (Fig. 6; see also Bailey, 1936: 3 and 4); 3) the ctenactinium is relatively large and externally evident; 4) the toxactinium is relatively slender and gently curved; and 5) the priapium itself may be either sinistral or dextral. In *Ph. posthon,* on the other hand, 1) the penis is smooth; 2) the penial skeleton has a large papillary bone but the penial bone is absent; 3) the ctenactinium, if it is present at all, is reduced and hardly detectable externally; 4) the toxactinium is stouter and distinctly more sharply curved; and 5) the priapium is invariably sinistral (toxactinium arising on left side) in the material examined.

Ph. posthon and *Ph. smithi* of both sexes can be distinguished at a glance by the position of the first dorsal fin relative to the anal fin base. In *Ph. posthon* the first dorsal (which has a single spine as in *Ph. smithi*) originates slightly posterior to the base of the last ray in the anal fin; in *Ph. smithi* it originates over the middle of the anal fin base. The first dorsal fin is somewhat closer to the second dorsal origin in *Ph. posthon* than in *Ph. smithi. Ph. posthon* is more elongate (depth of body at anal fin origin about 7, vs. 6 in *Ph. smithi*) and evidently a larger species. The average and maximum sizes of specimens in my two samples of *Ph. posthon* are definitely larger than in my two samples of *Ph. smithi* (which include specimens larger than those previously recorded). The largest male and female specimens of *Ph. smithi* are, respectively, 14.9 and 15.6 mm; of *Ph. posthon,* 17.0 and 18.0 mm (standard lengths). The largest specimens (both sexes) had a bright orange-yellow bar on the caudal peduncle, as in *Ph. smithi,*

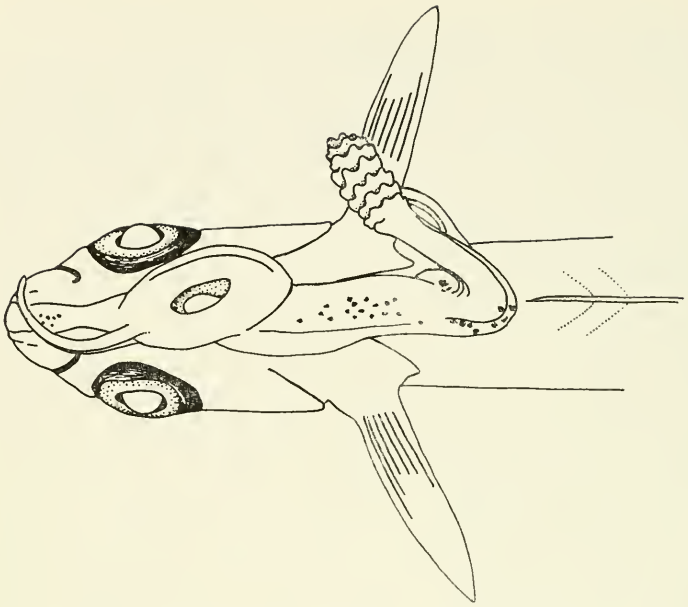

Figure 4. *Phenacostethus smithi* Myers (1928), ventral view of priapium, 14.1-mm specimen, MCZ 47055 (formalin).

and also a smaller orange-yellow bar on the body next to the anal fin origin.

As in *Ph. smithi,* there appears to be a one-to-one correspondence between the scale rows and the myotomes. The thin scales are extremely difficult to see in specimens under alcohol or water; and most specimens are missing many scales. I find in several specimens eight oblique scale rows between dorsal midline and anal fin origin, and six oblique scale rows between dorsal fin origin and anal base. Shape of jaw bones and disposition of teeth as in *Ph. smithi.*

For fin and vertebral counts based on alizarin preparations of *Ph. posthon* see Table 1. *Ph. posthon* seems to have, on the average, one less ray in the dorsal fin (verified by counts of unstained specimens) and one more vertebra than *Ph. smithi.*

Right- and left-handedness in the priapium of Phallostethidae.

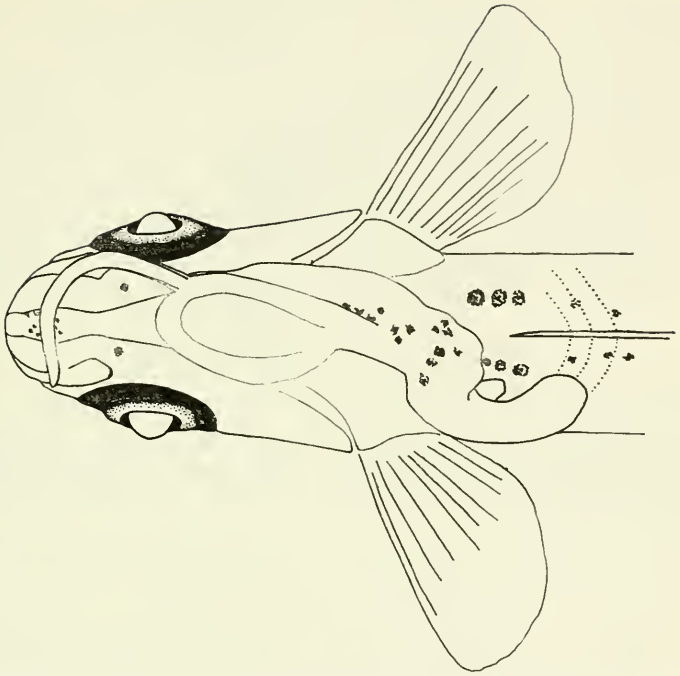

Figure 5. *Ph. posthon* n. sp., ventral view of priapium in 16.9-mm paratype, MCZ 47301 (formalin).

That the priapium of *Neostethus lankesteri* may be either right- or left-handed is stated by Regan (1916: 5). Regan did not specifically state that the priapium of *Phallostethus* may be either way, but in a general discussion of the priapium as compared to copulatory organs of other fishes, he refers to its being either dextral or sinistral (Regan, 1916: 23). Regan's figures of *Phallostethus* depict both right-handed and left-handed males. It is conceivable that one or more of them might be reversed images, the images being reversed either by the illustrator or by the printer, so the figures cannot be taken as definite proof that *P. dunckeri* may be either left-handed or right-handed. Concerning *Phenacostethus smithi,* Hubbs and Hubbs (1945: 294) found that in 334 males (from material collected by H. M. Smith at Bangkok)

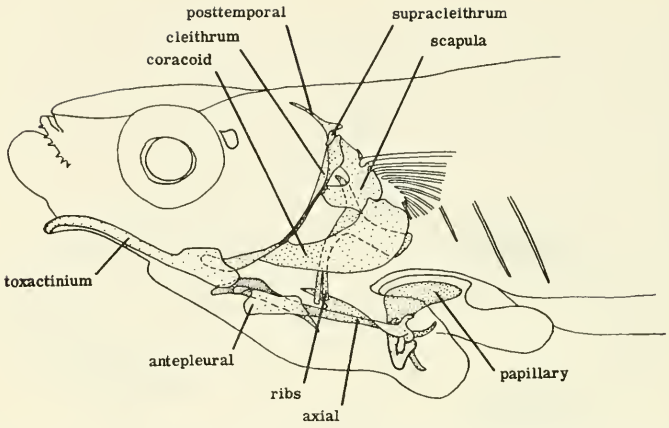

Figure 6. *Ph. smithi* Myers (1928), skeleton of priapium and pectoral fin in 14.5-mm specimen, MCZ 47301. Terminology of priapial elements according to Bailey (1936).

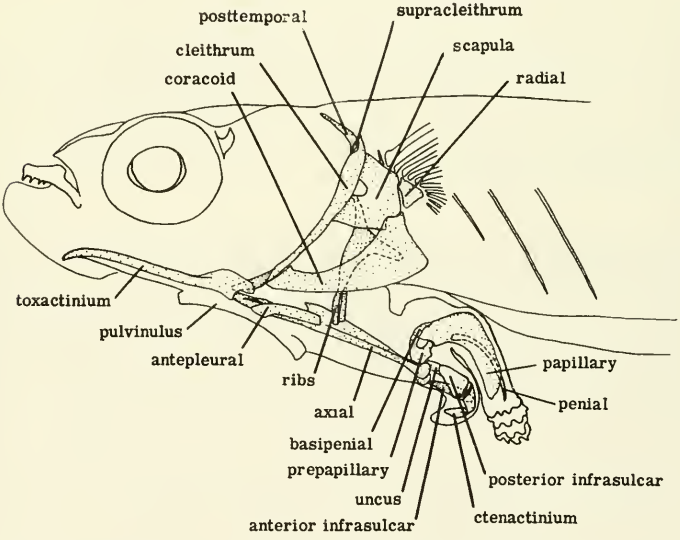

Figure 7. *Ph. posthon* n. sp., skeleton of priapium and pectoral fin in 16.5-mm paratype, MCZ 14301. Priapial elements of uncertain homology with those in *Ph. smithi* are unlabelled.

the aproctal side was the left side in 155 and the right side in 179. The deviation from equality is statistically insignificant. In my samples from Bangkhen and from Chantaburi (too small for statistical analysis) I find both left- and right-handed males. In *Phenacostethus posthon* the toxactinium arises on the left side in every male in which the priapium is sufficiently developed to have a toxactinium (27 specimens from Pungah and five from Satul). To my knowledge this is the only phallostethoid in which the sidedness of the priapium appears to be fixed. Females of Phallostethidae are bilaterally symmetrical, the genital openings lying in the middle of the throat.

ECOLOGICAL OBSERVATIONS

The only ecological information Regan had about *Phallostethus dunckeri* was that it came from brackish water from the Muar River at Bandar Maharani. Duncker also collected *Neostethus lankesteri* in the same general locality.

Smith (1927; 1945: 476) made brief ecological observations on *Phenacostethus smithi* but in restrospect it seems that he sometimes confused this little fish in the field with *Neostethus* or *Ceratostethus* and perhaps even with *Oryzias*. I did not observe either phallostethids or neostethids at the surface, and feel that they generally keep well below the surface. Smith's remarks (that *Phenacostethus* "normally remain at or close to the surface, where they would be difficult to see were it not for a glistening yellow area on the top of the head") sound more like *Oryzias*. The glistening area on the top of the head in phallostethoids is relatively small and bluish, compared to the large yellowish glistening area in *Oryzias,* which is comparable to the striking head spots in rivuline cyprinodontids of the genera *Epiplatys* and *Aplocheilus*. In any event, Smith records that *Ph. smithi* abounds in freshwater pools, ditches and smaller canals in the Bangkok region, living in water that is nearly always muddy or turbid, and that the species is oviparous (although spawning was not observed); the egg-bearing and spawning periods are protracted, corresponding with the rainy season, and may extend from May to December. Small numbers were maintained in aquaria for a month by the daily introduction of fresh ditch or canal water to provide food in the form of minute crustaceans, protozoans, worms, etc. Smith found the larvae of anopheline mosquitoes much too large for *Ph. smithi* to ingest.

Undoubtedly *Ph. smithi* once lived in innumerable khlongs and ditches in Bangkok which are today so polluted that they are inhabited only by the hardiest air-breathing fishes such as *Anabas testudineus*. In Khlong Bangkhen, a few kilometers from Kasetsart University, I found *Ph. smithi* in association with a variety of primary and secondary freshwater fishes, principal among which were cyprinids mainly of the genus *Rasbora, Dermogenys, Xenentodon, Oryzias, Gobiopterus chuno* (a small translucent goby), young *Fluta,* and *Chaudhuria*. The *Phenacostethus* were mostly in a little backwater, close to the main current in the khlong, in very turbid water. I was unable to taste any salt in the water. At Chantaburi City, *Phenacostethus* was collected in a turbid ditch or small khlong, Khlong Kee Nawn, behind the Catholic church. There were a number of houses along the khlong at this point, and considerable rubbish had been thrown into it, so collecting efforts were confined to dip-netting for *Phenacostethus. Dermogenys, Brachygobius* and *Gobiopterus* were collected incidentally. About two kilometers downstream, where the khlong traversed a large open field, we found minnows such as *Oxygaster, Esomus* and *Rasbora* (but no *Phenacostethus*) which indicates the water in the khlong was not brackish.

At Satul and at Pungah *Ph. posthon* was obtained along the margins of khlongs or tiny branches of khlongs in which the water was swiftly flowing, highly turbid, and probably completely fresh. A few of the largest females (collected June 1970) were replete with ripe ova. Both localities were at places fully subject to tidal fluctuations, but far upstream from branches having water the least bit salty to the taste. At Khlong Langu in Satul Province the water level was undoubtedly high because of heavy rains for the preceding 12 hours or more; *Phenacostethus* were collected in the khlong both on the falling tide and rising tide. No primary freshwater fishes were obtained. Species in the khlong where *Ph. posthon* was collected included *Oryzias, Dermogenys, Chanda, Gobiopterus, Butis,* and *Tetraodon*. In Khlong Kla Sohm, near Pungah, *Ph. posthon* was collected in a narrow side channel more or less uniformly 3–4 feet deep, swiftly flowing, with hard-packed mud bottom, well shaded by Nipa palm and mangrove. *Oryzias, Dermogenys, Gobiopterus, Periophthalmus, Tetraodon,* and young *Scatophagus* were the only other fishes collected or observed in this channel.

In contrast, on the more numerous occasions when I obtained either *Neostethus* or *Ceratostethus* in Thailand, the water was usually brackish or even very salty to the taste. At one locality *Neostethus* and *Ceratostethus* were collected together in large numbers but neither were collected in association with *Phenacostethus*. I did not find *Neostethus* or *Ceratostethus* in association with primary freshwater fishes except on one occasion (afternoon, 11 July 1970) when *Ceratostethus* was found in a khlong (strongly influenced by tides) about midway between Bangkok and Samutsakorn, in association with *Toxotes, Dermogenys, Rasbora* and *Esomus*. The water was more or less fresh to the taste. A number of dead *Esomus* were carried by the current of the khlong, and a *Rasbora* or two may have been amongst them. I thought at the time that mortality of these minnows was perhaps due to incursion of salt water. The dead fish were carried by the outgoing tide.

My impression is that, in Thailand, phallostethids occur in water that is turbid and fresh; and neostethids in water that is turbid and brackish or even quite salty. I would guess that at some of the seven localities where I collected neostethids the water was at least a third and perhaps one-half or more as salty as sea water.

The only phallostethoid in which mating and egg-laying have been observed (but not in sequence) is the neostethid *Gulaphallus mirabilis* Herre (Villadolid and Manacop, 1934). It seems probable that all phallostethoids are oviparous. No females carrying embryos have been observed. It is unclear how much time elapses between copulation and egg-laying in *G. mirabilis,* or whether several egg-layings follow a single copulation. Judging from the range in size of young individuals found with adults in my collections of phallostethoids, I suspect that in Thailand species some reproduction goes on throughout the year. It seems likely that reproductive peaks occur towards the latter part of the rainy season (November and December).

The distribution of phallostethoids is marginal to the rich East Indian marine and freshwater fish faunas. They do not occur in the sea, nor do they penetrate very far into fresh water where there is a continental fauna of primary freshwater fishes. The Phallostethidae penetrate further into waters inhabited by primary freshwater fishes than any other phallostethoids, but they do not

get very far inland. Usually the canals or creeks they inhabit are strongly influenced by tides, and thus the faunal composition (with regard to fishes at any rate) is subject to considerable temporal variation, involving retreat of primary freshwater fishes and invasion of brackish-water forms, and vice versa. In places where the tidal changes are greatest, these invasions and counterinvasions would be a daily event, varying of course with the extent in the tides. In other places they might occur only during the strongest tides. *Gulaphallus* on the island of Luzon probably pass their entire lives in fresh water—where no primary freshwater fishes occur.

DISCUSSION

Selective advantage of internal fertilization in phallostethoids. One usually associates copulatory organs in teleostean fishes with viviparity, as in Poeciliidae, Embiotocidae, and Brotulidae. It is a striking fact, however, that several groups of oviparous teleosts normally have internal fertilization. Among these are some Cottidae, some Scorpaenidae, probably some Clinidae, and probably some glandulocaudine characids. According to Nelson (1964) the evolution of internal fertilization in the oviparous glandulocaudine characids of tropical South America appears to be a response to well-marked wet and dry seasons. The presumed advantage of a temporal separation in mating and spawning is as follows: mating occurs during the dry season, when populations are crowded together in small pools, food is scarce and conditions for survival are generally unfavorable; spawning, on the other hand, occurs during the height of the rainy season, when the population is maximally dispersed (so much so that males and females may no longer be together) and conditions for survival of the young are optimum (abundance of food, well-oxygenated waters, access to areas where most predators are too large to enter). A very similar set of conditions may apply to the evolution of internal fertilization combined with oviparity in phallostethoids, with temporal separation of mating and spawning corresponding, respectively, with periods of low water and high water. This hypothesis should be extended to the oviparous atheriniform fishes *Horaichthys setnai* Kulkarni (1940) and *Tomeurus gracilis,* males of which have independently evolved excessively complicated copulatory organs through modification of the anal fin. *Tomeurus* occurs in brackish water along the northeastern coast of South

America, including the mouth of the Amazon River, *Horaichthys* in brackish water along the Bombay and Kerala coast of India. The sperm in *Tomeurus* are transmitted in spermozeugmata (Nielsen, et al., 1968: 253), as in the viviparous poecilioids (the nature of the phyletic relationship between *Tomeurus* and poecilioids is unclear; they probably are closely related). *Horaichthys,* on the other hand, is among the very few teleosts known to have a true spermatophore (Kulkarni, 1940; Nielsen, et al., 1968). (In true spermatophores the sperm are enclosed in a capsule. A spermozeugma is an unencapsulated group of sperm held together by a mucoid substance.)

Trends in the reproductive biology of atheriniform fishes that might be conducive to the evolution of internal fertilization. When oviparous fishes with internal fertilization exhibit a marked delay between mating and spawning, it may be presumed that fertilization actually occurs just before spawning, the sperm having been stored. Storage of sperm and delayed fertilization evidently characterize at least some viviparous fishes, such as those poecilioids (including forms with superfoetation and forms without it) in which females are capable of producing up to four or five successive broods after a single mating session. It should be noted, however, that the eggs of a number of atheriniform fishes with external fertilization normally exhibit arrested embryonic development or delayed hatching. A lengthening of the period between fertilization and hatching, particularly if it could be subjected to hormonal control, might be highly preadaptive to the evolution of internal fertilization with delayed spawning. While there is no evidence of arrested embryonic development or delayed hatching in atheriniforms with internal fertilization, it seems worthwhile to review briefly what is known about these phenomena in forms with external fertilization.

Wourms (1967) found that the eggs of annual cyprinodont fishes of the subfamily Rivulinae (*Cynolebias, Pterolebias, Rachovia, Nothobranchius,* and *Austrofundulus*) are subject to developmental arrest at one or more stages. In *Austrofundulus myersi* dispersion of amoeboid blastomeres occurs early in development (stages 19–22) so that there is no embryo or aggregation of cells. This is followed by a slow reaggregation of cells and resumption of development. This arrested phase (Diapause I) is facultative, and also occurs in other annuals. Obligate developmental arrests

in annuals were found in presomite embryos (stage 33, Diapause II) and in prehatching embryos (stage 44, Diapause III). The duration of these phases is rather variable. Wourms suggested that "the net effect of a developmental system which can undergo diapause of variable duration at several stages is to generate a wide distribution of eggs in any single developmental stage, and to make the transition from stage to stage a variable phenomenon. The continued survival of the population is ensured in spite of climatic cycles which are variable in periodicity and intensity" (Wourms, 1967: 3411). The eggs of annual cyprinodonts have exceptionally hard chorionic membranes. Harrington (1959) reported delayed hatching in stranded eggs of marsh killifish, *Fundulus confluentus,* a member of the cyprinodontid subfamily Fundulinae, and Jones (1944) reported delayed hatching in *Oryzias melastigma,* a member of the cyprinodontoid family Oryziatidae (see Rosen, 1964, for a characterization of this family). In *O. melastigma* hatching normally occurs in 8–14 days, yet can be delayed up to six weeks; hatching can be induced by adding water of lower salinity. The only noncyprinodontoid fishes in which delayed hatching has been reported as a normal phenomenon are one or two members of the atherinid subfamily Atherinopsinae, including the grunion, *Leuresthes tenuis.* In this species, "spawning begins just after turning of tide during the lower (bright moon) series of high tides, but somewhat later than turn of tide during the higher (dark moon) series of high tides. Thus the eggs are always deposited near the same point on the beach profile so that after 2 weeks the lower series of high tides washes out the eggs deposited during the higher series, and *vice versa.* During the interim of low tides, the eggs are above tide level in moist sand 4 inches below the surface" (Harrington, 1959: 434–435, after Thompson and Thompson, 1919; Clark, 1925). Grunion eggs presumably have a highly protective covering. It seems likely that more atheriniform fishes will be found with either delayed embryonic development or else deferred hatching (with viability of embryos sustained far beyond the usual incubation periods). The outer covering of the egg in many atheriniform fishes is highly protective. These reproductive features obviously could be advantageous to fishes such as cyprinodontoids, which generally exploit niches in ephemeral waters (Foster, 1967).

Finally, it should be noted that Laale and McCallion (1968) experimentally induced developmental arrest in *Brachydanio rerio,*

a cyprinid. Exposure to extracts from *Brachydanio,* frog, or chick embryos caused *Brachydanio* embryos at stages 17–18 to stop developing. Returned to buffered water, the embryos resumed normal development and hatched. Laale and McCallion suggested that the inhibitory factor might be a nuclease.

Foster (1967) suggested that in cyprinodontoids the shift from expelling and fertilizing all of the ovulated eggs in one continuous spawning act to expelling and fertilizing them singly or in small batches greatly increased the amount of courtship behavior per fertilized egg and thereby the impact of sexual selection. The habit of expelling a few eggs at a time is also found among atherinoids (see Breder and Rosen, 1966) and is apparently characteristic of phallostethoids (Villadolid and Manacop, 1934, for *Gulaphallus mirabilis;* Myers, 1935, for *Plectrostethus palawanensis*), *Horaichthys* (Kulkarni, 1940), and *Tomeurus* (Myers, 1947: 8–11; Breder and Rosen, 1966: 341–343). Whereas in many atheriniforms the tendency to deposit a few eggs at a time seems to have led to the evolution of prolonged courtship, in other lines it may have led to internal fertilization. Supposing females carry a fair number of eggs but lay only a few at a time, males that can impregnate the female and fertilize all of the eggs at once have an obvious selective advantage over males that can fertilize only a few eggs at a time. Even more to the point, there may be little to prevent the sperm from getting into the oviduct and fertilizing eggs retained inside the female. Thus, while fertilization normally is external in *Oryzias,* instances of *O. latipes* females with internally fertilized eggs (developing embryos) do occur (Amemiya and Murayama, 1931). *Oryzias* evidently is ancestral to *Horaichthys.*

Table 1.

	Second Dorsal	Anal	Caudal	Pectoral	Vertebrae
Ph. smithi (MCZ 47299)	II $4\frac{1}{2}$ (I $5\frac{1}{2}$?)	II $12\frac{1}{2}$	7 I 6 - 5 II 10	I 9	$14 + 20\frac{1}{2}$
" " "	II $4\frac{1}{2}$ (I $5\frac{1}{2}$?)	II $13\frac{1}{2}$	8 II 4 - 6 I 9	I 9	$14 + 19\frac{1}{2}$
Ph. posthon (MCZ 47301)	II $3\frac{1}{2}$ (I $4\frac{1}{2}$?)	II $12\frac{1}{2}$	8 I 4 - 4 II (5 I ?) 10	I 8	$15 + 20\frac{1}{2}$
" " "	II $3\frac{1}{2}$	II $12\frac{1}{2}$	8 I 4 - 4 II (5 I ?) 11	I 9	$16 + 19\frac{1}{2}$

Fin counts and vertebral numbers from alizarin stained and cleared male specimens of the two species of *Phenacostethus*. The distal end of the second element in the dorsal fin is not well developed (perhaps decalcified by maceration) so it is difficult to determine whether it is branched or unbranched; similarly, in some specimens it is difficult to determine the condition of the principal ray next to the outermost principal ray in the lower lobe of the caudal fin.

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STRUCTURAL HABITATS OF WEST INDIAN *ANOLIS* LIZARDS II. PUERTO RICAN UPLANDS

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ABSTRACT. This paper reports differences in structural and climatic habitat between the commonest *Anolis* species of two upland localities — Maricao and El Verde — in Puerto Rico.

Five of the seven *Anolis* species recorded at Maricao were studied in detail: two — *cristatellus* and *stratulus* — are major components of the warmer lowland fauna, and three — *krugi, evermanni,* and *gundlachi* — are representative of the cooler upland fauna. *A. stratulus* and *evermanni* tended to occupy higher and thicker perches than the other species; *krugi* was found on especially thin perches and often on leaves. The trunk-crown species *evermanni* and *stratulus,* of very different size, were virtually totally syntopic over the study area, while the trunk-ground species *cristatellus* and *gundlachi,* of very similar size, were virtually allopatric. Similarities and differences in climatic habitat between the species reflected this microgeography: *stratulus* and *evermanni* were found in fairly similar situations, though the former tended to be in opener areas, while *cristatellus* and *evermanni* were confined to open and closed habitats, respectively. At El Verde the same species were studied, but the open-area species *cristatellus* and *stratulus* were relatively rarer. Structural and climatic habitats paralleled those at Maricao, and the trunk-crown species were again more syntopic than the trunk-ground species.

In a separate analysis, it is shown that the two trunk-crown species had significantly more collecting localities in common than did the two trunk-ground species. The grass-bush species *pulchellus* and *krugi* were intermediate in this respect. It is hypothesized that the greater body size difference of the often syntopic trunk-crown species may be an adaptation preventing food overlap, an adaptation which the nonsyntopic trunk-ground species neither have nor need.

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The possible evolution of climatic and size differences is discussed for the upland and lowland series. It is suggested that in the broken, drier forest often found in the lowlands, the trunk-crown species would occur in more shaded conditions on the average than would the trunk-ground species: whereas in the wetter, more continuous forests of middle and upper elevations, the reverse situation would be true. Therefore, the trunk-crown species may have been predisposed for greater spatial overlap in advance of their coming together. That the lowland trunk-crown species should be smaller and less sexually dimorphic in size may be a result of greater average overlap between it and the corresponding trunk-ground species: possibly the lower average vegetation height and the greater need to avoid desiccation makes separation by height more difficult in the opener vegetation of the lowlands. No evidence to support this latter speculation is found in this study, however.

This is the second in a series of papers describing the structural habitats of some West Indian *Anolis* lizards. Rand (1964) has documented extensively differences between seven Puerto Rican species in their structural and climatic habitats. Our study will also elucidate gross interspecific differences, but its primary purpose is to demonstrate how the size classes of each species studied are deployed over the vegetation, with respect both to others of the same species and to similarly sized lizards of other species. Its secondary purpose is to investigate the spatial relationship between *stratulus* and *evermanni,* two "trunk-crown" forms (after Rand and Williams, 1969; Williams and Rand, in preparation) of very different size and sexual dimorphism, occurring in different but overlapping climatic and geographic areas.

FORMAT AND METHODS

Data on the structural habitat were gathered in the way described previously (Schoener and Schoener, 1971): for each lizard seen in the area, the type of perch, perch height, and perch diameter were noted. In addition, when the sun was shining the lizard was scored as to whether it perched mostly in the sun or shade. Observations during cloudy weather were lumped into a third climatic category. As before, the two of us simultaneously canvassed an area in staggered fashion so as to minimize the possibility of missing lizards. In addition, we were assisted during one afternoon at El Verde by E. E. Williams and W. P. Hall, III.

Results are presented here in two ways: 1) standard, structural habitat tables are given for each area and lizard class of interest (Tables 3–7), and 2) the occurrence in sun, shade or clouds is given for each of the same classes (Table 2).

In order to test for statistically significant differences in structural and climatic habitat between the lizard classes, the multiway contingency approach used previously (Schoener, 1970; Schoener and Schoener, 1971) was again employed. This procedure determines the strength of associations between the lizard classes and habitat variables while simultaneously taking into account possible associations between the habitat variables themselves. It is based on methods developed by Deming and Stephan (1940), Kullback (1959), and Bishop (1969), and is exposited for ecologists by Fienberg (1970); the appendix (page 18) outlines its particular application to our data. In addition, the appendix contains Tables 9–11, indicating the statistical significance of the comparisons we make below.

Our presentation begins with a description of the study sites and their anoline inhabitants, continues with a verbal summary of differences in habitat between the lizard classes, and terminates in a comparison of our results to previous ones and in a speculation on the evolution of size in relation to space for certain Puerto Rican anoles.

THE SPECIES

Ten species of *Anolis* are known from Puerto Rico (Table 1). These can be divided roughly into three groups on the basis of their climatic and correlated geographic ranges (Rand, 1964; Williams, Rivero and Thomas, 1965; Heatwole *et al.,* 1969; Webster, 1969).

One group comprises those species which occur modally in relatively humid, dark vegetation at high, cool elevations. This group consists of 1) *evermanni* — a medium-large, green, trunk-crown species, relatively sexually dimorphic in size; 2) *gundlachi* — a medium-large, rust-brown, relatively dimorphic trunk-ground species; 3) *krugi* — a small, striped yellow and brown, relatively dimorphic grass-bush species; and 4) *occultus* — a very small, grey-white, relatively nondimorphic twig species. Two of the three species, *evermanni* and *krugi,* are also found at scattered wet

lowland localities, probably in remnants of the nearly destroyed wet lowland forest.

The second group occurs modally in more illuminated, drier forest at the warmer low to moderate elevations. This group consists of 1) *stratulus* — a small, grey-brown, relatively nondimorphic trunk-crown species; 2) *cristatellus* — a medium-large, brown, relatively dimorphic trunk-ground species; and 3) *pulchellus* — a small, striped yellow and brown, relatively dimorphic grass-bush species. This group is also widespread in the highly disturbed wet lowlands and overlaps the first most commonly at mesic to wet intermediate altitudes, such as the Maricao locality to be described below. Additionally, George Drewry (personal communication) has found *cristatellus* predominating in high-altitude, mossy forest, most of which is above the altitudinal range of *gundlachi*.

The third group is restricted to the arid southwestern lowlands in xeric vegetation. It consists of 1) *cooki* — a medium-large, grey-brown, relatively dimorphic trunk-ground species, occurring sympatrically with *cristatellus* over much of its range; and 2) *poncensis* — a small, striped yellow and brown, grass-bush species of relatively moderate sexual dimorphism. Notice that in this group there is no trunk-crown representative.

A final species, the nondimorphic green giant *cuvieri*, appears from museum records to be commonest at middle and upland elevations, with pockets of abundance in the wetter lowlands such as those along the north coast.

LOCALITIES

The study to be reported below concentrates on the three commonest mostly upland species — *evermanni*, *gundlachi* and *krugi* — and two of the three commonest widespread species — *cristatellus* and *stratulus*. All five of these species were found in close proximity to one another in the Maricao Insular Forest, a preserve in the "monadnock" region (Pico, 1950) of the Cordillera Central. Consequently, several adjacent study sites of varying shapes were marked off in the preserve (altitude = 860–900 m, slightly less than 4 km due south of the town of Maricao), and the anoles were observed therein. We distinguished four such areas:

1. *Forest interior.* This area was the most natural of the four studied. It contained forest of medium height and somewhat

broken canopy, clinging to a 20–40° mountainside. The understory in many places was quite sparse and easily traversed, but where the canopy had broken, tangled grasses and ferns obstructed passage. The commonest species seen in this area was *gundlachi* (Table 2). The two trunk-crown species, *evermanni* and *stratulus,* were also common and appeared to be of nearly equal abundance. In addition, *krugi, cristatellus,* and *cuvieri* occurred as "trace" species. We saw no *occultus* though they have been collected there (Williams, Rivero, and Thomas, 1965).

2. *Forest with cleared understory.* This area was adjacent to the more undisturbed forest and consisted of a strip about 30–40 feet wide that bounded an open, grassy parking area. Although the understory had apparently been cleared, nearly all the large trees were left standing and very little sun penetrated to the ground, which itself consisted mostly of bare mud. In this area, *gundlachi* was again the most abundantly seen species, followed by *evermanni* and *stratulus,* again in nearly equal proportions. A few *cristatellus* were also seen at the edge of the area.

3. *Open forest.* This area was less elongated than Area (2) and faced it from directly across the parking area. Trees were arrayed in an open, parklike fashion; some overlaid a 2-to-3-foot herbaceous understory while others grew among short grass. Much sun penetrated to the ground, in contrast to Area (2). The most abundant species seen here was *cristatellus.* Again, *evermanni* and *stratulus* occurred in strikingly similar proportions. A few *gundlachi* were seen along the border between this area and Area (1). In addition, a few *krugi* inhabited the understory where it had not been chopped away.

4. *Secondary road edge.* This area comprised a strip about 10-20 feet wide bordering Area (1). The understory graded from a lawnlike growth to dense, tangled typical forest-margin vegetation. The area faced full sunlight during the morning hours, that time of day when the sun was most likely to be shining during the period of our study. Above the understory rose trees of varying heights, with 40- to 60-foot *Cecropia* emerging above the rest. This area showed the most equitable distribution of apparent abundances for the five species. *A. stratulus* was commonest, but *gundlachi* and *evermanni* were also rather frequently observed. Less abundant but far from rare were *cristatellus* and *krugi.*

We studied the Maricao area during the period June 23–26,

1969. Weather throughout this time was mostly sunny during the morning, generally partly cloudy during midday, and somewhat rainy during the afternoon — on one occasion in the form of a severe thunderstorm. Rainfall at the nearby but lower town of Maricao averages 111 inches per year (Pico, 1950).

To further elucidate the relationships between the upland species, a second, more humid area was investigated at El Verde in the Luquillo rainforest (340–440 m). The study sites were in parts of the forest that were and are still the subjects of intensive and extensive ecological investigation, including a study of its two commonest *Anolis* species by Turner, Gist, and Rowland (Odum, 1965). The area is described in detail in various reports (Odum, 1965; Kline, Jordan, and Drewry, 1967, 1968). In comparison to the Maricao forest, that at El Verde was considerably taller and of more continuous but still somewhat broken canopy; the understory was consequently sparser and there were frequent boulders strewn about the forest floor. Two study sites are distinguished in Table 2.

The first begins near the biological station and penetrates the interior of the forest along a trail that climbs upward, eventually terminating at an observation tower. Our records were all taken adjacent to the bottom third of the trail where the grade was closest to horizontal. This area was in coffee plantation until the early 1930's and had not reached climax but was still in middle succession at the time of our study (G. E. Drewry, personal communication). The second study site contained roadside secondary vegetation along the forest margin, very close to the first study area.

In both study areas, *gundlachi* was the species most frequently seen, although it appeared more dominant in the forest interior. The next most frequently encountered species was *evermanni,* relatively more abundant along the forest edge. Three other species, *stratulus, krugi,* and *cuvieri,* were rarely encountered in the forest interior; the first two were always observed in relatively open, sunny areas. The margin had, however, a more equitable distribution of species: *stratulus, cristatellus* and *krugi* did not appear uncommon. One *cuvieri* was also seen. All the relative abundances given in Table 2 are, of course, apparent only — they represent what we saw and are therefore biased in favor of three species (*gundlachi, cristatellus,* and *krugi*) frequently occurring at or below eye level.

Observations were made June 29 – July 1, 1969. Weather during this time was, in general, considerably overcast and rainy,

the rain occurring intermittently at all times of the day. Even though we tried to avoid sunless periods, a heavy incidence of clouds is apparent in Table 2. Rainfall in the vicinity was estimated from the weekly tables in Kline, Jordan, and Drewry (1967, 1968) as 189 inches per year from September 1964 through August 1966.

RESULTS

Differences between lizard classes. In the following discussion, all comparisons, unless otherwise stated, are statistically significant in the sense explained in the appendix. Each species dealt with is divided into two classes: 1) small individuals, comprising adult females, subadults, and juveniles, and 2) adult males. The great majority of the former class (85–100%) were too large to be labelled "juveniles."

Maricao open areas (Tables 3, 4, 9). In order to compare species classes from relatively open areas with respect to their structural and climatic habitats, observations from the "open forest" and "secondary road edge" were lumped together. Only the three commonest species of these areas — *evermanni, stratulus* and *cristatellus* — were treated statistically.

Male *evermanni* perched higher than did all other groups and were significantly higher than all but male *stratulus*. The latter class occurred higher than small *evermanni* or *cristatellus*. Small-sized *stratulus* were higher than small *evermanni* and all *cristatellus*. Small *evermanni* perched higher than either male or small *cristatellus*.

Male *evermanni* occurred on thicker perches than all other classes. Male *stratulus* were on thicker perches than all classes but male *evermanni*. Small *evermanni* were on thicker perches than small *stratulus* and small *cristatellus*. Male *cristatellus* occupied thicker perches than did small *stratulus*.

Within each of the three species, males perched on both higher and thicker branches than did small-sized individuals.

There were significant differences in the climatic habitats of *stratulus* males and the two classes of *cristatellus* (Table 2). The former occurred more often in the sun and less often in the shade than did either of the latter. There was also an overall tendency for male *stratulus* to be seen more often on cloudy days. Small *stratulus* too occurred more often in the sun than did either class

of *cristatellus* and were seen less often in the shade and on cloudy days. Small-sized *evermanni* were observed more often in the shade and less often on cloudy days than were male *stratulus;* sunny observations were of about equal proportions in the two classes. Small *evermanni* were seen more frequently in the sun than male *cristatellus* and less frequently on cloudy days; the percent observations in the shade were nearly identical. Small *evermanni* also occurred more frequently in sunny positions than did female *cristatellus;* the latter appeared more often during cloudy weather and, to a lesser extent, in the shade. No significant climatic differences were found between the classes of the same species.

Maricao closed area (Tables 5, 6, 10). Observations for two study sites, the interior forest and the forest with cleared understory, were lumped to compare the three most common species — *gundlachi, evermanni* and *stratulus.*

There was no significant difference in perch height between male *stratulus* and male *evermanni,* the two uppermost classes of anoles. Male *evermanni* were, however, seen significantly higher than small *stratulus* or the classes of *gundlachi.* Male *stratulus* did not differ significantly in height from small *evermanni* but were observed higher than either class of *gundlachi.* Small *evermanni* were seen slightly higher than small *stratulus* and all *gundlachi;* small *stratulus* also occurred higher than did the classes of *gundlachi.*

In perch diameter, male *evermanni* significantly exceeded all interspecific classes but male *stratulus.* Male *stratulus,* in turn, significantly exceeded all other interspecific classes but male *gundlachi.* Small *evermanni* were next in perch diameter, occupying thicker perches than either class of *gundlachi.* Small *stratulus* and male *gundlachi* were similar in perch diameter, and the former occurred on thicker perches than small *gundlachi.*

Once again, within the same species, the larger classes occurred on higher and thicker perches than did the smaller-sized classes.

Compared to the other species, both classes of *gundlachi* strikingly avoided sunny places. Small *gundlachi* were found significantly more often in the shade or on cloudy days than any class of *stratulus* or *evermanni.* Male *gundlachi* were found more often in the shade than small *stratulus,* and more often in the shade and on cloudy days than either class of *evermanni.* As was the case for the more open area, small *evermanni* were found considerably more often in the shade and less often during cloudy

weather than male *stratulus;* inside the forest, however, they were also seen slightly more often in the sun. In contrast to the opener areas, here small *evermanni* as well differed significantly in the above respects from small *stratulus*. No intraspecific comparisons were significant.

El Verde (Tables 7, 11). Observations for the two areas distinguished in Table 2 were combined to test structural habitat differences at El Verde. Only the two most abundant species, *evermanni* and *gundlachi,* were considered.

As before, male and small *evermanni* were higher than either class of *gundlachi.* Male and small *evermanni* also occupied thicker perches than did small *gundlachi.* Male *gundlachi,* however, were on greater-diametered perches than small *evermanni* and did not differ significantly from male *evermanni* in this respect, though the latter at Maricao occupied thicker perches. Intraspecifically, males once again were distributed over greater perch heights and diameters than small individuals.

There were no significant climatic differences between the lizard classes — this is unsurprising because of the small sample size and preponderance of cloudy weather at El Verde.

The common species at El Verde, *evermanni* and *gundlachi,* are similar in size and sexual dimorphism (Table 1) and appear to stagger their sizes in such a way as to overlap most small *evermanni* and large *gundlachi,* with respect to both perch height and perch diameter.

The situation becomes more complex where a third species, *stratulus,* is more abundant, as in the Maricao interior forest. The two species *evermanni* and *gundlachi* still maintain the same spatial relationship between their size classes. However, male *stratulus* are now inserted between male *evermanni* and small-sized *evermanni.* They differ markedly from the former in size (Table 1) but are only slightly smaller than the latter. There is also rather strong overlap between small *stratulus* and small *evermanni;* the latter, however, average a good bit larger. Small *stratulus* also extensively overlap male *gundlachi* but are very different in size. They differ greatly in both perch height and diameter from the similarly sized small *gundlachi.*

In the opener areas at Maricao, the situation is essentially the same for both diameter and height except that *cristatellus* virtually replaces *gundlachi.* Given that substitution, the only difference

that appears to exist is a reversal in relative height of small *stratulus* and small *evermanni*. This reversal allows a more nearly perfect staggering of sizes: now male *stratulus* are further from small-sized *evermanni*. All overlaps, of course, are further reduced by the existence of climatic differences between the niches of the species.

It is important to point out that in many places in the lowlands *evermanni* is absent; there, presumably, *cristatellus* and *stratulus* often stagger their sizes in much the same way as do *evermanni* and *gundlachi*. However, even if the classes of adult males overlapped the most (see below), the two lowland species probably do not take very similar food since they are so different in size — in contrast to *gundlachi* and *evermanni*. Moreover, it is interesting to note that where *stratulus* and *evermanni* overlap extensively, as at Maricao, there is only a slightly greater tendency than at "pure" upland or lowland localities for similarly sized classes to overlap, as a result of the great difference in size between the two trunk-crown species.

Because of their small sample size, classes of *krugi* were not tested against any other. However, if all observations for *krugi* from the three areas are lumped, and to these are added observations made in high grass and other secondary growth near the mid-elevation town of Adjuntas, it is possible to compare large and small *krugi* in structural habitat. Table 8 shows that males of *krugi* occurred significantly higher and on thicker diameters than did small-sized lizards. However, even more striking was the much greater frequency of small *krugi* on leaves. This result is consistent with those for other species that occupy the leaf habitat in a major way: *carolinensis* on Bimini (Schoener, 1968) and *grahami aquarum* on Jamaica (Schoener and Schoener, 1971). No climatic difference was found between the two classes.

Differences between habitat variables (Tables 9–11). In the Maricao open area the only significant height-diameter associations were those in which thinner perches tended to be high and thicker perches tended to be low. Fewer comparisons were significant in the interior forest at Maricao, but those that were showed a uniformly opposite tendency. This could easily reflect our observational bias: fewer lizards can be seen in the canopy when within the forest. The one significant interaction at El Verde was the same as those for the Maricao closed area.

In the open area at Maricao, there was a tendency, when we combined male-*evermanni* perches with those of interspecific classes, for the highest perches to occur in the sun and the lowest in the shade, as would be expected from the physiognomy of the vegetation. A somewhat different result was true for the three significant interactions in the interior vegetation: high perches were more often used on cloudy days; the lowest perches were still more frequently found in the shade, however. At El Verde, the one significant interaction (for male *evermanni* vs. small *gundlachi*) was the same as those for the Maricao open area.

There were no significant interactions at all between perch diameter and insolation in the Maricao closed area, and only one such interaction was significant for the Maricao open area. This was a tendency for the combined perches used by small *stratulus* and small *cristatellus* to be thinnest in the sun and thickest on cloudy days. At El Verde, in contrast, perches of male *evermanni* and male *gundlachi* were significantly thickest in the sun and thinnest in the shade. The combined perches for male *evermanni* and male *gundlachi* also were thinnest in the shade, but the thickest perches were used during cloudy weather. Both these interactions may again primarily represent the greater ease of seeing a lizard on the thin branches and twigs of the understory than on similarly sized branches belonging to the high canopy of the El Verde rainforest. They could, however, also reflect real differences in utilization of the habitat by lizards: for example, during the rather brief sunny periods at El Verde, lizards may have moved onto broader surfaces to bask more effectively.

CONCLUSION

Although we have concentrated on differences between the size classes of the lizards at Maricao and El Verde, our results for species agree well with those reported by Rand (1964) in his pioneering study of the structural habitat of species from all areas of Puerto Rico. In that study Rand pointed out the size difference between the two trunk-crown species, *stratulus* and *evermanni,* and suggested that, because of their similarity in climatic habitat (as measured by body and air temperature, as well as shade vs. sun records), these two species should in general show a greater amount of spatial overlap than the trunk-ground or grass-bush

species. Although in an area near the town of Maricao the few *stratulus* seen by Rand did not seem to overlap *evermanni* much in horizontal habitat, we have shown above that in our areas at the Maricao Insular Forest, the two species were quite syntopic and sometimes were of nearly identical apparent abundance (Table 2). Thus we saw 62 *evermanni* and 66 *stratulus* in the forest interior, 20 *evermanni* and 17 *stratulus* in the forest with cleared understory, 70 *evermanni* and 72 *stratulus* in the open forest, and 36 *evermanni* and 138 *stratulus* along the road edge. Even at our study site at El Verde, where *evermanni* was seen more frequently (67 *evermanni* and 7 *stratulus* in the interior and 31 *evermanni* and 11 *stratulus* along the forest margin), *stratulus* was interspersed throughout *evermanni's* horizontal range, although in the interior it was seen only in fairly open places, such as on sunny spots along the trail, high on emergent trees, and on streamside boulders. G. E. Drewry (personal communication) has, however, seen *stratulus* more commonly than *evermanni* in the more closed, relatively less leafy canopy of certain other areas at El Verde.

The extensive syntopy of the trunk-crown species is in striking contrast to the trunk-ground species we studied. For example, in the forest interior at Maricao we saw 243 *gundlachi* and 1 *cristatellus*. In the open forest at Maricao we saw 175 *cristatellus* and 8 *gundlachi*. In the interior forest at El Verde we saw 243 *gundlachi* and 0 *cristatellus*. All three of these areas were relatively equilateral in shape. In the more elongated, marginal areas we saw more equitable proportions of the two: 33 *gundlachi* and 6 *cristatellus* in the forest with cleared understory at Maricao, 50 *gundlachi* and 25 *cristatellus* along the Maricao secondary road edge, and 51 *gundlachi* and 14 *cristatellus* along the edge locality of El Verde. At the second of these areas, where the numbers are closest to identity, we noted that along a strip about ten feet wide *cristatellus* and *gundlachi* were perching upon the same vegetation, although under different climatic conditions: *cristatellus* was especially common during sunny days, whereas the majority of the *gundlachi* individuals were seen under overcast skies. Thus, even though there is spatial overlap of *cristatellus* and *gundlachi* in marginal areas, it is largely nonsynchronous.

We can test differences in the relative abundances of trunk-ground vs. trunk-crown species by constructing 2×2 contingency

tables and running chi-square or exact tests. If this is done for the six study areas, it is seen that the relative proportions of the two trunk-ground species are significantly different from those of the two trunk-crown species in the El Verde interior forest, Maricao interior forest, Maricao road edge, and Maricao open forest at the 1 percent level and in the Maricao forest with cleared understory at the 5 percent level. Only the ecomorphs in the El Verde forest margin show nonsignificant differences in proportions. In summary, we can conclude that at our study sites the trunk-ground species were practically allopatric, whereas the trunk-crown species overlapped broadly.

There exists a second way in which the degree of horizontal spatial overlap between the species belonging to various habitat categories may be detected. Museum localities are usually distinguished horizontally, that is, as points on a map. Therefore, we have listed all the localities at which specimens of the six common Puerto Rican species from the Museum of Comparative Zoology (Harvard) and the University of Michigan Museum have been collected. There were 91 such localities for *cristatellus* and *gundlachi* combined, and only 7 of these (7.7%) were held in common between the two species. In contrast, 9 of 45 localities (20%) were held in common between *evermanni* and *stratulus*. This proportion was significantly different by a chi-squared test ($P < 0.05$). The grass-bush species, *krugi* and *pulchellus*, were intermediate in this regard: 8 of 59 localities (13.6%) were held in common. This proportion did not differ significantly from trunk-crown or trunk-ground species. While the comparisons involve the error that not all species inhabiting a given locality will be taken by collectors, usually because of differential abundance and/or accessibility, that error should counteract the pattern brought out in this analysis. That is to say, because the two trunk-crown species are seen less often and are more difficult to capture, there is less likelihood of both being collected at any given locality than both trunk-ground forms.

It therefore appears clear that the relatively great body-size difference between the trunk-crown species in Puerto Rico is associated with their relatively great spatial overlap. Presumably this size difference in part helps the species to avoid resource competition by being associated with and facilitating differences in the diet, especially with regard to prey size. However, while the association is presumably adaptive, the mechanism whereby it came

about is unclear. That is, did the species differ in size to begin with and so were able to overlap spatially when they came together to a great degree, or were the size differences largely evolved in response to a predisposition for spatial overlap in the trunk-crown forms? We can crystallize the relevant problems by asking three questions:

1. (a) Why should any of the three structural habitat groups — trunk-crown, trunk-ground, and grass-bush — contains species which differ markedly in size? (b) Why should it be the trunk-crown group, and that only, which contains such species? There is thus an existence and uniqueness part to this question.
2. Given that the trunk-crown species show the greatest size differential, why should the lowland dry-area form be the smaller, and the upland wet-area form be the larger?
3. Why should the lowland trunk-crown species be much less sexually dimorphic in size than the upland species?

We can gain some insight into the first question by ranking separately for upland and lowland forest the modal habitats of the three kinds of species on a darkness or humidity or coolness gradient (we assume the three to be highly correlated). In middle and upper elevation forest, such as that at El Verde and Maricao, the darkest vegetation is the understory, and the most exposed vegetation lies along margins and in the canopy. Therefore we would expect the trunk-ground species, which primarily inhabit the lowest layer of the forest, to be better adapted to dark, cool conditions than either the trunk-crown species — found largely in the canopy or somewhat lower — or the grass-bush species, found mostly along margins. However, the situation is different for the lowland forest. Much lowland forest in Puerto Rico, particularly in the south, is and must have been for some time of xeric aspect. It is characteristic of such forest, as well as of much coastal woodland elsewhere, to have a relatively broken canopy, with much light penetrating to the understory and with the largest trees being often quite dispersed. The patchiness is intensified during the dry season by some but not all trees undergoing partial or complete leaf drop. The darkest places for an arboreal lizard in such vegetation are often associated with the largest trees,

especially often within or directly under the crown. Although that fraction of the understory immediately beneath such trees will also usually be shaded, the average degree of shading of the understory as a whole should be considerably less than in the humid forest of middle and upper elevations. The grass-bush habitat should be even less shaded. Consequently, the trunk-crown habitat should in the lowlands be *on the average* the darkest and coolest; the trunk-ground habitat should be intermediate and the grass-bush habitat should be on the average the hottest and most illuminated, even though there are places in these latter two habitats as shaded as any in the crown and on the upper trunk. It also follows that within the lowland trunk-ground habitat, there should be a greater diversity of shade regimes than in the upland trunk-ground habitat. This implies that in the lowlands large adult males, which prefer thick perches, are more likely to find such perches shadier than the average small-diametered perch preferred by the females. This difference should scarcely exist for the upland species. Therefore, there should be a greater intersexual difference in climatic habitat for the lowland trunk-ground form than for the upland trunk-ground form.

Matching species with structural habitat and combining the upland and lowland species into a single ranking, as would be appropriate for the many intermediate localities on the island, we should obtain from sunniest to shadiest: *pulchellus* > *cristatellus* > stratulus >= *evermanni* = *krugi* > *gundlachi*. Notice that the trunk-ground and grass-bush species are widely separated, but that the trunk-crown species are adjacent. That is, the lowland trunk-crown species should occur in the darkest part of its habitat and the upland trunk-crown species in the sunniest part of its habitat. Consequently, there should be a great deal of spatial overlap in intermediate areas on the basis of climatic habitat alone. This means that much of the size difference could well have evolved as a necessary adjunct to climatic preferenda of the trunk-crown species, preferenda which have developed independently of one another as adaptations to the prevalent vegetational structure. No such size difference need have evolved for the trunk-ground or grass-bush species, farther apart on the climatical spectrum.

The temperature data of Rand (1964, fig. 4), particularly those for the air, fit for the most part the inequality stated above. Thus,

among the primarily lowland species, *pulchellus* occurs at the warmest temperatures, *cristatellus* at cooler temperatures, (with great variance, perhaps because of intersexual differences) and *stratulus* the coolest. Almost identical to *stratulus* is *evermanni,* whereas *gundlachi* is about the same as *evermanni* and therefore warmer than predicted, possibly because the highest *evermanni* could not be sampled. Values for *gundlachi* fall below the bulk of the *cristatellus* observations. Air temperatures for *krugi* are somewhat higher than those for *evermanni* but markedly below the majority of the *pulchellus* observations.

Rand (1964) also provides information on species within five localities as to their degree of occurrence in shade. This again depicts *stratulus* and *evermanni* as differing little, while the other groups differ a good deal. Also shown is that *cristatellus* and *stratulus* can be fairly similar in their shade occurrences, though in all cases *stratulus* occupied the deeper shade. *A. gundlachi* and *evermanni* are, however, very different, the former being, of course, more often in shady positions. In the two localities where both *krugi* and *pulchellus* were found, they showed practically no overlap in their shade occurrences.

The climatic data we have gathered at Maricao, which are of a different sort than those presented by Rand, also support the greater similarity of the trunk-crown species in their climatic habitats than the trunk-ground forms. There is not even any consistent tendency for one or the other of *stratulus* or *evermanni* to be found more often in the sun among the Maricao localities, although *evermanni,* if any, appears commoner there. This may in part, of course, be an artifact of observation; at El Verde, as we judge from the few *stratulus* data, the situation appeared to be reversed. The two trunk-ground species cannot be compared in most places because one or the other is nearly absent, but along the secondary road edge, as mentioned, *gundlachi* was much more likely to be seen during cloudy weather. At El Verde, despite the preponderance of overcast skies, *cristatellus* were seen several times more frequently in the sun than *gundlachi.*

A second aspect of the above scheme that can be checked from our data is the climatic relation between trunk-ground and trunk-crown forms. Although *evermanni* and *gundlachi* showed striking differences in the expected direction, *stratulus* and *cristatellus* did not. In fact, *stratulus* were seen significantly more often in the

sun in the open area at Maricao (see above). Possibly this was an artifact of observation, but it is more likely that in the shade *cristatellus* perches averaged warmer than did those of *stratulus* because of the more exposed nature of the vegetation on which it perched. But Heatwole (1968; Heatwole *et al.,* 1969) showed that individuals of *stratulus* and *cristatellus* in "an open park-like situation" at Rio Piedras did not differ significantly in their air or substrate temperatures. However, Heatwole *et al.* (1969) have found that even under apparently identical mean environmental temperatures, the body temperatures of *stratulus* average lower than those of *cristatellus.* Furthermore, *cristatellus* shows greater resistance to high temperatures and does not tolerate low ones as well as *stratulus.*

Heatwole *et al.* conclude both from these physiological properties and Rand's data that "although the two species have similar ecologies and distributions, in some cases coexisting under apparently identical conditions, there is a tendency for *A. cristatellus* to utilize the warmer (less shaded) habitats than *A. stratulus.*" Their conclusion agrees well with the scheme we have outlined above.

The second question posed above may be related to the relative degree of overlap between trunk-ground and trunk-crown forms in the two areas. If we could show that the lowland species are more likely to overlap spatially than the upland forms, then we could argue that the smaller size of *stratulus* may have evolved in part as a response to that overlap and thus served as a preadaptation for any further displacement that might have occurred between the trunk-crown species. Rand's structural habitat grids show practically no differences in percent overlap (62.5% vs. 61%) between the two species pairs. However, his data were from several localities and all size classes combined. Even if only adult males are considered and our data for particular localities used, results are inconsistent: percent overlap for *evermanni* and *gundlachi* is 35 percent in the forest interior at Maricao and 72 percent at El Verde, whereas that for *stratulus* and *cristatellus* is 30 percent along the Maricao road and 50 percent in the Maricao open forest. It is possible that these results are artifacts of the greater difficulty of seeing a trunk-crown species in the canopy when within a continuous forest than when along a forest margin or in a very open area. That error would tend to minimize differences between *evermanni* and *gundlachi* and is almost certainly

in part responsible for the high overlap value at El Verde. One might argue, *a priori,* that because of the greater average height of rainforest such as that at El Verde, overlap between two species segregated mainly by height should be less than in drier forest. Furthermore, even though the species are physiologically adapted to different thermal environments, it is possible that in the dry lowlands the greater danger of desiccation forces *cristatellus* and *stratulus* together in shaded situations during a large portion of the day; in the uplands, however, no such problem need arise, and the more exposed species, in this case *evermanni,* can occur in sunny or open places most of the day. This is perhaps the reason why less difference was found between the climatic habitats of *cristatellus* and *stratulus* than between *gundlachi* and *evermanni* in our study. Any overlap between the first pair should be especially severe for male *cristatellus* because they more frequently occupy the relatively large trees which *stratulus* inhabit.

If the explanation above be correct, that is, had *stratulus* evolved small size in part to alleviate competition with male *cristatellus,* then the reduced sexual dimorphism of *stratulus* would automatically follow, since it is the male that would be displaced.

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STATISTICAL APPENDIX

This appendix briefly reiterates the description of the statistical treatment of the structural and climatic habitat data given in detail elsewhere (Schoener and Schoener, 1971). Four variables — lizard class, climatic category, perch height and perch diameter — were used to set up 4-way contingency tables. For the lizard and

climatic variables, two (the classes being compared) and three (sun, shade, and clouds) categories (levels), respectively, were used. For perch height and diameter, two levels each were chosen by separately determining the point of maximum difference in cumulative frequency between the distributions of the habitat variable for the two lizard classes being compared. Data were broken at this point, all observations less than or equal to that number being cast into one category and all greater than that number being cast into the other. Table 12 lists critical values for height and diameter groupings. As before, an iterative procedure (Deming and Stephan, 1940; Bishop, 1969; Fienberg, 1970) was used to fit the data to models containing all six 2-way interactions. One by one, interactions were dropped if differences between models were not significant at the 5 percent level according to difference in the log-likelihood ratio chi-square (Kullback, 1959; Ku and Kullback, 1968). Results are summarized in Tables 9–11. The following key applies to the numbers in the body of the table:

1 — the interaction was significant every time it was tested in the removal procedure;

2 — the interaction was significant at least at the termination of the procedure;

3 — the interaction was significant when removed from the most inclusive model (with six interactions) but not at termination;

4 — the interaction was significant sometime during the procedure but not at the beginning or end;

0 — the interaction was never significant.

As can be seen, nearly all interactions could be labelled "0" or "1." There was no set of models for a particular 4-way table which never gave a χ^2 value denoting a satisfactory fit of the model at the 5 percent level, regardless of what interactions were removed. Therefore we did not test for 3-way interactions. There were only three tables with zero margins. These could be, and therefore were, handled in the way given by Fienberg (1970).

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TABLES

Table 1. The sizes and habitats of Puerto Rican *Anolis* species.

	Driest Areas (southwest corner)		Intermediate Areas (mostly low and middle elevations)		Wettest Areas (mostly middle and upper elevations)	
	♂	♀	♂	♀	♂	♀
Trunk-crown[1]	(some *stratulus*)		*stratulus*		*evermanni*	
			46.7 mm	39.9 mm	70.7 mm	52.4 mm
Trunk-ground	*cooki*		*cristatellus*		*gundlachi*	
	59.5 mm[2]	41.6 mm	66.4 mm	44.6 mm	64.8 mm	45.2 mm
	(some *cristatellus*)					
Grass-bush	*poncensis*		*pulchellus*		*krugi*	
	45.6 mm	39.6 mm	46.9 mm	37.0 mm	49.7 mm	39.3 mm
Twig					*occultus*	
					39.0 mm	39.2 mm
Giant			*cuvieri*			
			131.3 mm	119.4 mm		

[1] Based on Williams and Rand (in prep.); see Rand and Williams (1969) for list of categories.

[2] Snout-vent length means of largest third of all specimens examined; see Schoener (1969).

Table 2. Climatic and geographic occurrence of Puerto Rican anoles.

Lizard Class		Percent Occurrence				Sample Size	Percent Composition
		Sun	Shade	Clouds	Sun or Shade		
Maricao, forest interior							
evermanni	adult male	53.8	11.5	34.6	0	26	6.9
evermanni	small	44.4	22.2	27.8	5.6	36	9.6
gundlachi	adult male	17.1	34.3	45.7	2.9	70	18.7
gundlachi	small	15.6	32.4	48.0	4.0	173	46.1
stratulus	adult male	31.8	4.5	63.6	0	22	5.9
stratulus	small	31.8	13.6	47.7	6.8	44	11.7
cristatellus	adult male	0	0	100.0	0	1	0.3
cristatellus	small					0	
krugi	adult male	50.0	0	50.0	0	2	0.5
krugi	small					0	
cuvieri	large					1	0.3
Maricao, forest, cleared understory							
evermanni	adult male	0	16.7	83.3	0	6	7.9
evermanni	small	28.6	57.1	14.3	0	14	18.4
gundlachi	adult male	0	25.0	75.0	0	8	10.5
gundlachi	small	0	16.0	84.0	0	25	32.9
stratulus	adult male	33.3	0	66.7	0	6	7.9
stratulus	small	9.1	18.2	72.7	0	11	14.5
cristatellus	adult male					0	
cristatellus	small	66.7	33.3	0	0	6	7.9
krugi	adult male					0	
krugi	small					0	
cuvieri	large					0	

Lizard Class		Percent Occurrence				Sample Size	Percent Composition
		Sun	Shade	Clouds	Sun or Shade		
Maricao, open forest							
evermanni	adult male	33.3	28.6	33.3	4.8	21	6.2
evermanni	small	44.9	28.6	20.4	6.1	49	14.5
gundlachi	adult male					0	
gundlachi	small	12.5	50.0	25.0	12.5	8	2.4
stratulus	adult male	40.5	8.1	45.9	5.4	37	11.0
stratulus	small	22.9	37.1	37.1	2.9	35	10.4
cristatellus	adult male	22.0	26.0	50.0	2.0	50	14.8
cristatellus	small	22.4	32.0	41.6	4.0	125	37.1
krugi	adult male	28.6	42.9	28.6	0	7	2.1
krugi	small	0	60.0	40.0	0	5	1.5
cuvieri	large					0	
Maricao, secondary road edge							
evermanni	adult male	78.3	0	21.7	0	23	8.3
evermanni	small	69.2	7.7	23.1	0	13	4.7
gundlachi	adult male	11.1	27.8	61.1	0	18	6.5
gundlachi	small	15.6	3.1	78.1	3.1	32	11.5
stratulus	adult male	55.6	7.4	33.3	3.7	54	19.4
stratulus	small	59.5	8.3	31.0	1.2	84	30.2
cristatellus	adult male	33.3	33.3	16.7	16.7	6	2.2
cristatellus	small	36.8	21.1	31.6	10.5	19	6.8
krugi	adult male	0	25.0	50.0	25.0	4	1.4
krugi	small	4.0	16.0	76.0	4.0	25	9.0
cuvieri	large					0	
El Verde, interior							
evermanni	adult male	5.6	33.3	61.0	0	18	5.6
evermanni	small	3.9	27.6	68.6	0	51	15.7
gundlachi	adult male	7.1	32.5	59.8	0.6	169	52.2
gundlachi	small	5.4	41.9	52.7	0	74	22.8

stratulus	adult male	100.0	0	0	0	1	0.3
stratulus	small	33.3	33.3	33.3	0	6	1.9
cristatellus	adult male					0	
cristatellus	small					0	
krugi	adult male	50.0	0	50.0	0	2	0.6
krugi	small	0	0	100.0	0	4	1.2
cuvieri	small	0	0	100.0	0	1	0.3
El Verde, edge							
evermanni	adult male	46.2	23.1	30.8	0	13	9.5
evermanni	small	27.8	16.7	55.6	0	18	13.1
gundlachi	adult male	8.3	36.1	52.8	2.8	36	26.3
gundlachi	small	13.3	26.7	60.0	0	15	10.9
stratulus	adult male	67.7	0	33.3	0	3	2.2
stratulus	small	37.5	12.5	37.5	0	8	5.8
cristatellus	adult male	50.0	0	50.0	0	6	4.4
cristatellus	small	25.0	25.0	50.0	0	8	5.8
krugi	adult male	16.7	16.7	66.7	0	6	4.4
krugi	small	21.7	26.1	52.2	0	23	16.8
cuvieri	small	100.0	0	0	0	1	0.7

Table 3. Maricao secondary road edge. Percent observations in various structural habitat categories. H = >20'; G = ground; R = rocks; N = sample size.

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 54	male stratulus	H = 11	G = 0	R = 0		
10.5-20	4	17	4	0	0	25
5-10	9	17	6	0	0	32
3-4 3/4	9	4	4	0	0	17
<3	9	4	4	0	0	17
Total	31	42	18	0	0	
N = 84	small stratulus	H = 2	G = 0	R = 0		
10.5-20	4	8	7	1	0	20
5-10	4	13	13	6	0	36
3-4 3/4	2	6	5	5	0	18
<3	10	6	6	1	2	23
Total	20	33	31	13	2	
N = 6	male cristatellus	H = 0	G = 0	R = 0		
10.5-20	0	0	0	0	0	0
5-10	0	0	0	0	0	0
3-4 3/4	17	17	0	0	0	34
<3	33	17	17	0	0	77
Total	50	34	17	0	0	
N = 19	small cristatellus	H = 0	G = 11	R = 0		
10.5-20	0	0	0	0	0	0
5-10	0	0	0	0	0	0
3-4 3/4	5	0	0	0	0	5
<3	16	26	26	16	0	84
Total	21	26	26	16	0	

N = 23	male evermanni		H = 4	G = 0	R = 0	
10.5-20	22	17	0	0	0	39
5-10	9	13	0	0	4	26
3-4 3/4	17	0	0	0	0	17
<3	13	0	0	0	0	13
Total	61	30	0	0	0	

N = 13	small evermanni		H = 0	G = 0	R = 0	
10.5-20	0	8	0	0	0	8
5-10	0	15	0	0	8	23
3-4 3/4	8	0	0	0	0	8
<3	46	15	0	0	0	61
Total	54	38	0	0	8	

Table 4. Maricao open forest. Percent observations in various structural habitat categories. H = >20'; G = ground; R = rocks; N = sample size.

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 37	male stratulus		H = 0	G = 0	R = 0	
10.5-20	0	22	0	0	0	22
5-10	8	16	11	5	0	40
3-4 3/4	3	3	0	5	0	11
<3	5	19	3	0	0	27
Total	16	60	14	10	0	
N = 35	small stratulus		H = 0	G = 0	R = 0	
10.5-20	0	3	0	0	0	3
5-10	3	6	19	13	0	41
3-4 3/4	9	0	11	9	0	29
<3	14	9	6	0	0	29
Total	26	18	36	22	0	

N = 50	male cristatellus		H = 0	G = 6	R = 0	
10.5-20	0	6	0	0	0	6
5-10	4	4	10	2	0	20
3-4 3/4	8	0	12	2	0	22
<3	20	10	7	7	2	46
Total	32	20	29	11	2	

N = 125	small cristatellus		H = 0	G = 12	R = 1	
10.5-20	0	2	0	0	0	2
5-10	0	2	5	2	0	9
3-4 3/4	2	2	2	3	1	9
<3	11	23	16	15	2	67
Total	13	29	23	20	3	

N = 21	male evermanni		H = 0	G = 10	R = 0	
10.5-20	5	19	7	2	0	33
5-10	5	5	14	5	0	29
3-4 3/4	10	5	0	0	0	15
<3	14	0	0	0	0	14
Total	34	29	21	7	0	

N = 49	small evermanni		H = 6	G = 2	R = 0	
10.5-20	2	6	2	4	0	14
5-10	4	6	12	10	0	32
3-4 3/4	0	2	4	0	0	6
<3	16	10	8	2	2	38
Total	22	24	26	16	2	

Table 5. Maricao forest with cleared understory. Percent observations in various structural habitat categories. H = >20'; G = ground; R = rocks; N = sample size.

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 6	male	stratulus	H = 50	G = 0	R = 0	
10.5-20	0	17	0	0	0	17
5-10	17	17	0	0	0	34
3-4 3/4	0	0	0	0	0	0
<3	0	0	0	0	0	0
Total	17	34	0	0	0	
N = 11	small	stratulus	H = 0	G = 0	R = 0	
10.5-20	0	9	0	0	0	9
5-10	9	18	9	9	0	45
3-4 3/4	0	0	0	0	0	0
<3	18	18	9	0	0	45
Total	27	45	18	9	0	
N = 8	male	gundlachi	H = 0	G = 0	R = 0	
10.5-20	0	0	0	0	0	0
5-10	0	12	12	25	0	49
3-4 3/4	0	12	0	12	0	24
<3	0	0	19	6	0	25
Total	0	24	31	43	0	
N = 25	small	gundlachi	H = 0	G = 0	R = 0	
10.5-20	0	0	0	0	0	0
5-10	4	4	4	4	0	16
3-4 3/4	0	16	8	4	0	28
<3	4	12	28	12	0	56
Total	8	32	40	20	0	

N = 6	male evermanni		H = 0	G = 0	R = 0	
10.5-20	17	0	0	0	17	34
5-10	0	33	17	0	0	50
3-4 3/4	0	0	0	0	0	0
<3	0	17	0	0	0	17
Total	17	50	17	0	17	
N = 14	small evermanni		H = 0	G = 7	R = 0	
10.5-20	0	0	0	0	0	0
5-10	7	14	14	0	0	35
3-4 3/4	0	0	0	0	0	0
<3	36	21	0	0	0	57
Total	43	35	14	0	0	

Table 6. Maricao forest interior. Percent observations in various structural habitat categories. H = >20'; G = ground; R = rocks; N = sample size.

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 22	male stratulus		H = 5	G = 0	R = 0	
10.5-20	0	32	5	0	0	37
5-10	5	14	7	11	5	42
3-4 3/4	0	0	9	0	0	9
<3	5	5	0	0	0	10
Total	10	51	21	11	5	
N = 44	small stratulus		H = 2	G = 2	R = 0	
10.5-20	2	2	2	2	2	10
5-10	5	5	16	11	7	44
3-4 3/4	0	0	2	2	0	4
<3	2	9	20	2	2	35
Total	9	16	40	17	11	

N = 70	male gundlachi		H = 0	G = 1	R = 0	
10.5-20	0	0	0	0	0	0
5-10	4	4	6	4	0	18
3-4 3/4	1	11	13	7	1	33
<3	9	11	11	13	1	45
Total	14	26	30	24	2	

N = 173	small gundlachi		H = 0	G = 8	R = 1	
10.5-20	0	0	0	0	0	0
5-10	1	1	0	3	0	5
3-4 3/4	0	1	5	4	1	11
<3	3	9	23	29	11	75
Total	4	11	28	36	12	

N = 26	male evermanni		H = 8	G = 0	R = 0	
10.5-20	15	4	8	0	0	27
5-10	12	12	12	8	0	44
3-4 3/4	0	8	0	0	8	16
<3	8	0	0	0	0	8
Total	35	24	20	8	8	

N = 36	small evermanni		H = 3	G = 3	R = 0	
10.5-20	0	8	11	0	0	19
5-10	0	6	17	14	3	40
3-4 3/4	0	3	6	3	3	15
<3	0	6	8	8	0	24
Total	0	23	42	25		

Table 7. El Verde. Percent observations in various structural habitat categories. H = >20'; G = ground; R = rocks; N = sample size.

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 205	male gundlachi		H = 0	G = 2	R = 1	
10.5-20	0	3	0	0	0	3
5-10	15	10	12	7	0	44
3-4 3/4	8	12	9	3	0	32
<3	9	4	2	1	0	16
Total	32	29	23	11	0	
N = 89	small gundlachi		H = 0	G = 4	R = 3	
10.5-20	0	0	0	0	0	0
5-10	0	8	8	6	1	23
3-4 3/4	4	5	9	10	0	28
<3	6	12	9	12	0	39
Total	10	25	26	28	1	
N = 31	male evermanni		H = 0	G = 3	R = 0	
10.5-20	6	0	6	0	0	12
5-10	16	3	10	6	3	38
3-4 3/4	13	3	13	0	0	29
<3	10	3	3	0	0	16
Total	45	9	32	6	3	
N = 69	small evermanni		H = 1	G = 6	R = 3	
10.5-20	6	1	0	1	1	9
5-10	1	4	12	9	6	32
3-4 3/4	4	3	3	9	0	19
<3	13	9	2	4	0	28
Total	24	17	17	23	7	

Table 8. A. krugi, all localities combined. Percent observations in various structural habitat categories. H = >20'; G = ground; R = rocks; N = sample size.

Ht. (feet) \ Diameter (in.)	>5	5-2 1/2	2 1/4-7/8	7/8-1/8	leaves	Total
N = 33	male krugi	H = 0	G = 0	R = 0		
10.5-20	0	3	0	3	0	6
5-10	0	0	6	30	15	51
3-4 3/4	0	0	12	6	6	24
<3	0	0	3	12	3	18
Total	0	3	21	51	24	
N = 83	small krugi	H = 0	G = 4	R = 0		
10.5-20	0	0	0	0	0	0
5-10	0	0	0	1	5	6
3-4 3/4	0	0	0	7	16	23
<3	0	0	2	11	54	67
Total	0	0	2	19	75	

Table 9. Statistical significance for Maricao open area comparisons.[a]

Group vs. height / Group vs. diameter	male *stratulus*	small *stratulus*	male *cristatellus*	small *cristatellus*	male *evermanni*	small *evermanni*
male *stratulus*		1	1	1	0	1
small *stratulus*	1*		1	1	1*	1
male *cristatellus*	1*	0		1	1*	1*
small *cristatellus*	1*	1*	1*		1*	1*
male *evermanni*	1	1	1	1		1
small *evermanni*	1*	1	0	1	1*	
Group vs. insolation / Height vs. diameter						
male *stratulus*		0	1(C*)	1(C*)	0	1(D*)
small *stratulus*	0		1(C*)	1(C*)	0	0
male *cristatellus*	0	1(B)		0	0	2(D*)
small *cristatellus*	0	1	1(B)		0	1(C)
male *evermanni*	0	0	0	0		0
small *evermanni*	1(B)	1(B)	0	1(B)	1(B)	

Diameter vs. insolation \ Height vs. insolation						
male *stratulus*		0	0	0	1(F)	0
small *stratulus*	0		0	0	1(F)	0
male *cristatellus*	0	0		0	1(F)	0
small *cristatellus*	0	1(J)	0		2(F)	0
male *evermanni*	0	0	0	0		0
small *evermanni*	0	0	0	0	0	

[a] * = species at top has larger value; B = small diameters at higher perches; C = more in shade and clouds; D = more in shade and sun; F = highest in sun and lowest in shade; J = thinnest in sun and thickest in clouds; for interpretation of numbers, see "Statistical appendix."

Table 10. Statistical significance for Maricao interior area.[a]

Group vs. height / Group vs. diameter	male stratulus	small stratulus	male gundlachi	small gundlachi	male evermanni	small evermanni
male stratulus		1	1Z	1	0	0
small stratulus	1*		1	1	1*	4*
male gundlachi	0	0		1	1*	1*
small gundlachi	1*	1*	1*		1*	1*
male evermanni	0	1	1	1		1
small evermanni	1*	0	2	1	1*	
Group vs. insolation / Height vs. diameter						
male stratulus		0	0	1(C*)	0	1(D*)
small stratulus	1(A)		1(E)	1(C*)	0	1(D*)
male gundlachi	1(A)	0		0	2(C)	1(C)
small gundlachi	0	0	0		1(C)	1(C)
male evermanni	0	0	0	0		0
small evermanni	0	1(A)	0	0	0	

Diameter vs. insolation \ Height vs. insolation						
male stratulus		0	1(K)	0	0	2(K)
small stratulus	0		0	0	0	0
male gundlachi	0	0		0	0	0
small gundlachi	0	0	0		0	0
male evermanni	0	0	0	0		2(K)
small evermanni	0	0	0	0	0	

[a] * = species at top has larger value; A = small diameters at low perches; C = more in shade and clouds; D = more in shade and sun; E = more in sun and clouds; K = thickest in sun and thinnest in shade; Z = has zero margins; for interpretation of numbers, see "Statistical appendix.")

Table 11. Statistical significance for El Verde.[a]

Group vs. height / Group vs. Diameter	male evermanni	small evermanni	male gundlachi	small gundlachi
male evermanni		1	2	1
small evermanni	1*		1*	1
male gundlachi	0	1		1
small gundlachi	1*	1*	1*	
Group vs. insolation / Height vs. diameter				
male evermanni		0	0	0
small evermanni	0		0	0
male gundlachi	0	0		0
small gundlachi	1(A)	0	0	
Height vs. insolation / Diameter vs. insolation				
male evermanni		0	0	1(F)
small evermanni	0		0	0
male gundlachi	1(K)	0		0
small gundlachi	2(L)	0	0	

[a] * = species at top has larger value; A = small diameters at low perches; F = highest in sun and lowest in shade; K = thickest in sun and thinnest in shade; L = thinnest in shade and thickest in clouds; for interpretation of numbers, see "Statistical appendix."

Height (feet) / Diameter (inches)	male stratulus	small stratulus	male cristatellus	small cristatellus	male evermanni	small evermanni
Maricao open area						
male stratulus		12	5	2 3/4	4	1 1/2
small stratulus	2		4 3/4	2 1/4	9	2 3/4
male cristatellus	2	4		2 1/4	9	6 1/4
small cristatellus	2 3/4	5/8	4		3 1/2	2 1/4
male evermanni	4	4	4	4		3 1/2
small evermanni	1 1/2	3 1/2	3	3	4	
Maricao closed area						
male stratulus		6	6 3/4	4 1/4	10	6
small stratulus	3		5	4 3/4	8 1/2	7
male gundlachi	3	3/4		2 1/4	6 3/4	6 3/4
small gundlachi	3	1 3/4	2 1/4		6	4 3/4
male evermanni	5	2	2	2		8 1/2
small evermanni	3	1 1/4	7/8	1	1 3/4	

Height (feet) / Diameter (inches)	male gundlachi	small gundlachi	male evermanni	small evermanni
El Verde				
male gundlachi		3 1/2	5 3/4	3 1/2
small gundlachi	7/8		3 1/2	5
male evermanni	3	1 1/2		4
small evermanni	5	4	1 1/2	

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Podocnemis venezuelensis, a new fossil pelomedusid (Testudines, Pleurodira) from the Pliocene of Venezuela and a review of the history of *Podocnemis* in South America

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and

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ABSTRACT. *Podocnemis venezuelensis*, a new species of pelomedusid turtle from the mid-Pliocene (Huayquerian) of Venezuela is described. Present evidence is insufficient for determining whether it was a marine or a fresh water form. Previously described South American fossil species that have been attributed to *Podocnemis* are discussed. Of these, only two — *P. bassleri* and *P. elegans* — are surely referable to this genus. It is concluded that the fossil record of *Podocnemis* is not yet adequate for reconstructing its evolutionary history on this continent.

RESUMEN. Se describe una nueva especie de tortuga pelomedusida del Plioceno medio (Huayqueriense) de Venezuela, *Podocnemis venezuelensis*. Las presentes pruebas son insuficientes para determinar si fué de aguas marinas o de agua dulce. Se discuten las especies suramericanas fósiles que han sido atribuidas a *Podocnemis*. De estas, solo dos — *P. bassleri* y *P. elegans* — son valederas. Se concluye que el registro fósil de este genero no es aún adecuado para la reconstrución de su historia evolutiva en este continente.

INTRODUCTION

Only one species of fossil turtle, *Podocnemis geologorum* (Simpson, 1943), has ever been formally described from Venezuela. Other occurrences of Venezuelan fossil chelonians have,

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however, occasionally been mentioned: Swinton (1928) referred three specimens "too fragmentary for specific determination," of Pliocene or Pleistocene age (Van Frank, 1957: 22n), to "*Testudo* sp."; and Royo y Gomez (1960) published a faunal list of fossil vertebrates discovered in what is now known as the upper member of the Urumaco Formation, that included ". . . varios caparazones completos . . . de tortugas palustres (*Podocnemys*) . . . ." which he believed to be of mid-Miocene age. Unfortunately, the untimely death of Royo y Gomez in 1961 prevented his describing any of this material. The specimens, however, are preserved in the collections of the Universidad Central de Venezuela in Caracas. Except for one report on rodent remains (Pascual and Diaz de Gamero, 1969) and another on a new gavial (Sill, 1970), nothing has been published on them. The fossil turtles are described here.

Abbreviations used in this paper are:

AMNH — the American Museum of Natural History, New York

MCN — Museo de Ciencias Naturales, Caracas

VF — Laboratorio de Paleontologia, Escuela de Geologia de la Facultad de Ingeniera de la Universidad Central de Venezuela (Caracas).

CLASSIFICATION AND DESCRIPTION

Order **Testudines**

Suborder **Pleurodira**

Family **Pelomedusidae**

Genus **Podocnemis**

A cautionary word is appropriate concerning the attribution of fossil material to *Podocnemis.* Most extinct species of this genus are known solely from shell material. However, at least one other fossil genus, *Bothremys,* has a shell that is virtually indistinguishable from that of *Podocnemis.* In fact, two purported species of *Podocnemis, P. barberi* (Schmidt, 1940) and *P. alabamae* (Zangerl, 1948), were originally described on the basis of shell material that, upon the later discovery of associated skull material, has subsequently been referred to the genus *Bothremys* (Gaffney and Zangerl, 1968). Conceivably, therefore, when skulls become known for some of the fossil species now referred to *Podocnemis*

on the basis of their shells, it may be necessary to transfer them elsewhere. The new species described in this paper is placed in *Podocnemis* with this caveat.

Podocnemis venezuelensis sp. nov.
(Figures 1–3 and Plates I–V)

Type. VF 1176, a complete carapace, slightly flattened, including much of the axial buttresses and the pelves, the latter badly damaged. Also, VF 1173, a fairly complete but badly fractured plastron lacking only the entoplastron and epiplastra. Although bearing a different number, the plastron is of an appropriate size and state of preservation so that we believe it highly probable that both of these shell elements are from the same individual (see Plate IV). Unfortunately, none of Royo y Gomez's notes contain information bearing on this point.

Hypodigm. The type, and VF 1174, a plastron lacking the posterior lobe; VF 1175, the anterior one-third of a carapace; VF 1177, a complete carapace and plastron, considerably flattened, of a relatively small individual; VF 1177a, a nearly complete carapace and plastron of the largest individual in the sample, lacking only the pygal and posterior portions of both eleventh peripherals; VF 1177b, the left epiplastron, hyoplastron, and left one-half of the entoplastron, plus several pleurals attached to part of the bridge, probably all belonging to the same individual; VF 1059, the distal end of a right humerus.

Horizon and locality. The "capa de huesos" or "capa de tortugas" (Pascual and Diaz de Gamero, 1969: 373 and map) of the upper member of the Urumaco Formation, probably of mid-Pliocene (Huayquerian) age, north of Campo El Mamón, state of Falcón, Venezuela.

The Uramaco Formation is divided into three members, designated as lower, middle, and upper. The lower and middle members are largely, if not entirely, of marine origin while the upper member apparently includes both littoral or deltaic as well as more strictly terrestrial facies. Marine molluscs from the middle member were the basis for the original age determination of mid-Miocene for this formation. This was subsequently revised to late Miocene. However, the recent study of Pascual and Diaz de Gamero (1969: 379) indicates that at least the "bone bed" of the uppermost part of the upper member is probably of middle

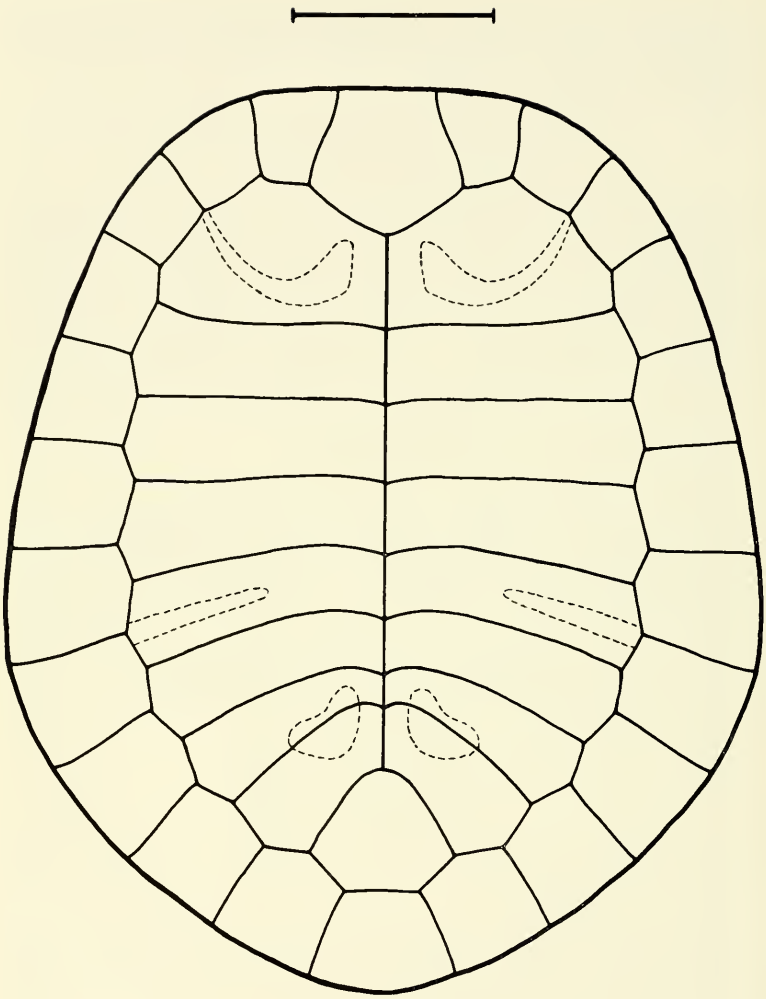

Figure. 1 Reconstruction of the shell of *Podocnemis venezuelensis* (dorsal view). The scale represents a length of 15 centimeters. The positions of the axial and inguinal buttresses as well as of the iliac scars of the pelvis on the visceral surface of the carapace are indicated by the broken lines.

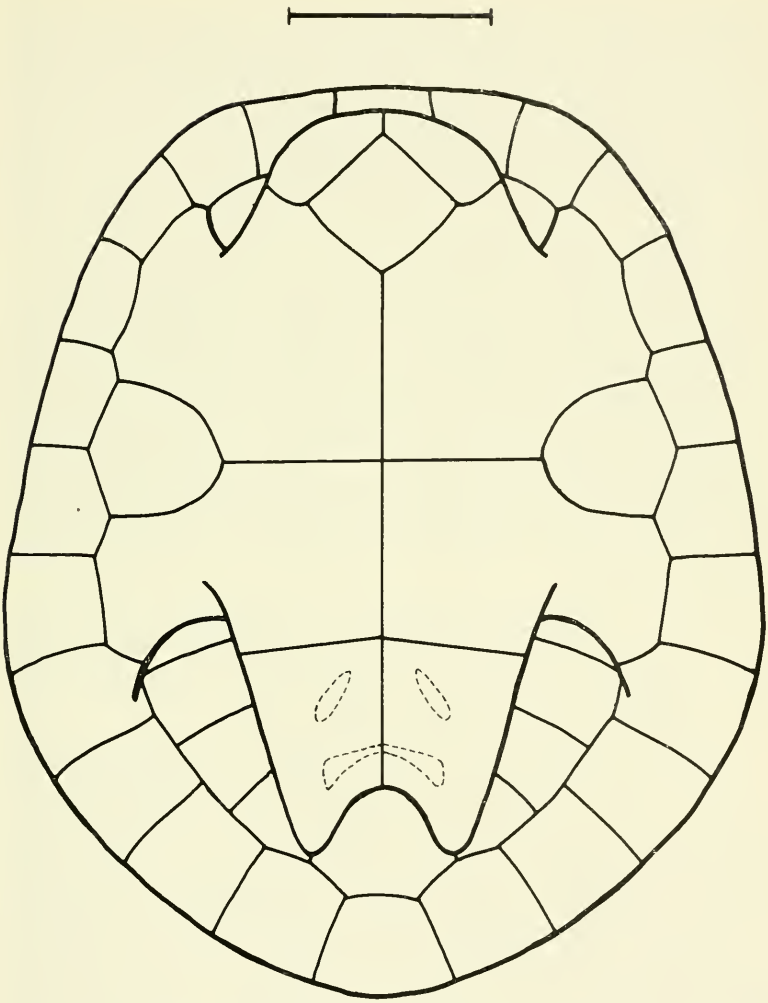

Figure 2. Reconstruction of the shell of *Podocnemis venezuelensis* (ventral view). Same scale as in Fig. 1. The positions of the pelvic scars on the visceral surface of the plastron are indicated by the broken lines.

Pliocene (Huayquerian) age. Palynological evidence appears to confirm this date (A. E. González Guzmán, personal communication). It is possible that there may be a temporal hiatus between the middle and upper members of the Urumaco Formation that cannot be detected structurally; an explanation of this nature would account for the different age determinations of the middle and upper members of the Urumaco Formation.

Diagnosis. Differs from all other species of *Podocnemis* in totally lacking neural bones.

Description. It is unfortunate that a gypsiferous encrustation on the external surfaces of all of the specimens obscures most of the bone sutures and virtually all scute sulci. Nevertheless, an essentially complete osteological description of the shell is possible from examination of the visceral surfaces of the type and some other, less complete specimens. Although the outlines of any particular bone may differ somewhat from the external to the internal surface of the shell, as Dacqué (1912: 290 and fig. 7) has demonstrated, it is nonetheless possible to make a reasonable reconstruction of the shell of a typical representative of the species (see Figures 1 and 2).

Adult specimens of *Podocnemis venezuelensis* attained a rather large size. The three complete carapaces in our sample range from approximately 46 to 67 centimeters[1] in length. Of the eight living species of *Podocnemis,* only two, *P. expansa* and *P. unifilis,* are reported to reach a larger maximum size.

In cross section, the arch of the carapace is very flat; in outline it is somewhat oval and greatly expanded posteriorly. The external surface of the carapace is completely smooth. No significant indentation occurs in the nuchal region. Well-developed axial and inguinal buttresses unite the carapace to the plastron. The plastron itself is essentially flat and of nearly uniform thickness throughout.

The outstanding feature of the carapace, and indeed the character permitting definition of a new species, is the complete absence of neural bones. Otherwise, the carapace is typical of other South American representatives of the genus. The nuchal bone is roughly pentagonal and slightly broader than long in its maximum dimensions; its postero-lateral borders are bowed outwards

[1] The larger number represents the estimated total length of VF 1177a; its actual midline length as preserved is 60.1 centimeters.

slightly. There is no indentation at the midline of the anterior margin. The eight pairs of pleurals meet in the midline. As in all pelomedusids, there are eleven pairs of peripherals. The pygal is trapezoidal and the suprapygal is roughly subtriangular. Buttresses of the axial and inguinal notches are attached to the undersides of the first and fifth pleurals respectively. The iliac scars of the pelvis are situated on the visceral surfaces of the seventh and eighth pair of pleurals.

Of the three elements of the plastron, the bridge is the longest while the anterior lobe is the shortest. The anterior plastral lobe is U-shaped and does not extend beyond the anterior lip of the carapace. The lateral margins of the posterior lobe are straight rather than curved and are inclined medially so that the posterior lobe becomes narrower toward the rear. The entoplastron is diamond-shaped and has a slight U-shaped ridge with the open end facing anteriorly on its visceral surface; this is presumably for the attachment of neck muscles. At the midline junction of the epiplastra there is a pronounced protuberance on the visceral side. The mesoplastra are subrounded to hexagonal elements situated

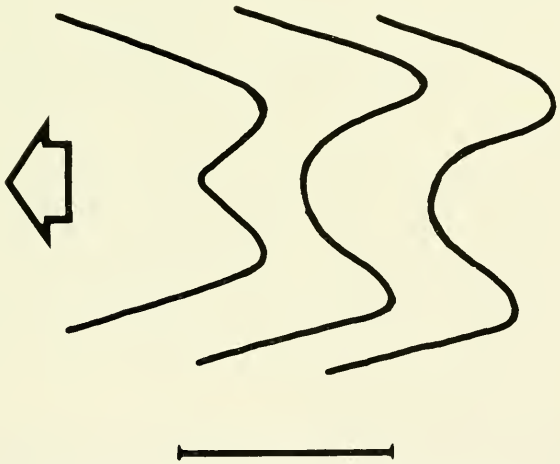

Figure 3. The shape of the anal notch in three specimens of *Podocnemis venezuelensis* (from left to right, VF 1177, VF 1173 and VF 1177a). The arrow points toward the anterior end of the shell. The scale represents a length of 10 centimeters.

laterally at the base of the bridge. (These can best be observed on the internal surface of VF 1174; see Plate V.) There is some variation in the shape of the anal notch; in the smallest specimen, VF 1177, it is V-shaped, but in the two larger examples, VF 1173 and VF 1177a, it is broader at its base and thus tends to be more U-shaped (Fig. 3). This structural difference may be due to sexual dimorphism. If so, however, it is not possible to specify which type represents the males and which the females in this species. Normally, male turtles can be distinguished from females by the characteristic depression on the posterior lobe of their plastrons, but it is not possible to determine whether or not these existed in the present sample because, in the course of fossilization, all the plastra have been somewhat depressed inward along the midline. Size alone is not a useful criterion for identifying the sexes in *Podocnemis*. In all but one of the living South American species of this genus mature females are invariably larger than males. The reverse is true, however, for *P. dumeriliana* (F. Medem, personal communication). Nor does the shape of the anal notch necessarily provide a reliable method of sex determination. Although in at least one species, *P. lewyana,* males can be identified solely on the basis of this character, there are other species (e.g., *P. vogli*) in which the two sexes appear to have similarly shaped anal notches, while in still others (e.g., *P. unifilis*) the shape of the anal notch varies considerably but evidently also randomly with respect to sex.

Pelvic scars on the plastron appear to be disposed in essentially the same positions as in the living South American species. Although partial pelves have been preserved in several of the specimens (VF 1173, 1176, 1177, and perhaps also 1177a), none of these are well enough preserved to describe in detail.

The distal half of a right humerus (VF 1059) is all that is known of the appendicular skeleton. Nothing serves to distinguish this limb fragment from comparable portions of this same bone in other species of *Podocnemis*.

Virtually no scute sulci can be detected in any of the specimens available for study. This is disappointing because their arrangement, particularly on the anterior plastral lobe, is sometimes of taxonomic significance.

DISCUSSION

Taxonomic considerations. Within the suborder Pleurodira, the presence or absence of neural bones has been accorded varying taxonomic significance. Those chelyid species that do possess neurals usually have a variable number, and in certain species of this family neurals evidently may or may not be present in different individuals of the same population. Consequently, whether or not a chelyid carapace includes some neurals, and if so, how many, has never been considered a useful taxonomic character[1]. Most pelomedusid species, however, have a neural series that does not deviate from a modal number (usually 6–8) by more than one or, occasionally, two. Only two exceptions to this typical condition are known within the family, both involving extinct taxa from the Eocene of Tunisia[2]. *Gafsachelys* (de Stefano, 1903; Bergounioux, 1952; 1955; 1956), like some chelyids, appears to have had a rather variable number of irregularly shaped neurals. *Eusarkia* (Bergounioux, 1952; 1956), described on the basis of a single specimen, has no neurals and on the basis of this and several other characters noted by Bergounioux we believe that it was probably appropriate to propose a new genus. But in no case has the absence of neurals alone been used as a taxonomic character, either at the generic or the specific level, within the Pleurodira (or among any other chelonians for that matter).

Why, then, have we described the Urumaco fossil pelomedusids as a new species of *Podocnemis?* In view of their strong overall resemblance to the living South American species of this genus it seems inappropriate to propose a new genus on the basis of a single character which, by itself, is not highly unusual nor of particularly great taxonomic significance among other members of the suborder. On the other hand, since the absence of neurals is clearly a constant character within the Venezuelan sample, this

[1] No adequate osteological descriptions of any living chelyid species have ever been published, so that reliable data are not actually available regarding the extent of intraspecific variation in the number of neurals.

[2] One of us (RCW) is preparing a discussion of the taxonomic status of the Tunisian fossil turtles for publication elsewhere. In this paper *Euclastochelys* (Bergounioux, 1955; 1956) is considered to be synonymous with *Gafsachelys*.

feature can hardly be regarded as an aberrant condition of no taxonomic consequence. Thus, by a process of elimination, the only alternative is to choose a procedure intermediate between regarding the lack of neurals as of enormous taxonomic importance or as of none at all and describe the Venezuelan material as a new species.

Ecological considerations. The small vertebrate fauna with which *Podocnemis venezuelensis* is associated (Royo y Gomez, 1960: 509; Pascual and Diaz de Gamero, 1969: 370 and 374) is not adequate for determining with any degree of certainty what the probable habitat of this species might have been. The mammals — a eumegamyine rodent and a toxodontid — were undoubtedly strictly terrestrial forms, while the crocodilians presumably spent most of their time in streams, lakes, or swamps. The fish — sharks, sawfish, rays, catfish, and an unidentified teleost — appear to be a mixture of marine and fresh water forms. If all these fossils were collected from a single horizon, as the scanty field evidence would suggest, then the stratum in which they occur must represent an estuarine facies. On the basis of present evidence, therefore, it is impossible to determine unequivocally whether *P. venezuelensis* was a marine or a fresh water form. To be able to do so would be particularly interesting because, while all living pelomedusids are inhabitants of fresh waters, in the past some were marine and others were fresh water forms (Wood, MS). If *P. venezuelensis* were, in fact, marine, it would be the last recorded pelomedusid so adapted.

No living species of *Podocnemis* (or any other fresh water turtle) are found in the Maracaibo basin, in which the type locality of *P. venezuelensis* lies, although they are common to the south and east of this enclave in Venezuela as well as to the west of it in Colombia. Thus, *P. venezuelensis* occurs outside the present range of the genus. Should *P. venezuelensis* eventually prove to be a fresh water rather than a marine form, its extinction may be explicable in terms of the Pleistocene climatic history of tropical South America. The Maracaibo basin is ringed by mountains except on its seaward side and hence is effectively isolated from adjacent land areas. Conceivably, a period or periods of aridity during the Pleistocene (and evidence for severe climatic fluctuations in the tropics during this epoch is accumulating — cf. Vanzolini and Williams, 1970: 94–103) may have eliminated *P.*

venezuelensis, a form presumably endemic to the basin, while the surrounding mountain barrier prevented subsequent recolonization by other species.

The fossil record of Podocnemis in South America. Few fossil species of *Podocnemis* have been described from this continent and several of these are known from such inadequate material that it is questionable whether or not they should be referred to the genus.

As previously noted, Simpson (1943) has described a partial carapace and plastron from Venezuela as *Podocnemis geologorum*[1]. The single known specimen was recovered from fluviatile beds of Miocene age. Without a doubt, this fossil represents some kind of pleurodire because of the union of its pelvis with both carapace and plastron. Whether this specimen actually represents a pelomedusid instead of a chelyid, however, is not entirely clear. Although Simpson (1943: 57) commented "Es muy posible la existencia en esta especie de un mesoplastrón tipo *Podocnemis* de buen tamaño," the presence or absence of this pair of bones, the critical character for distinguishing members of one pleurodiran family from the other, cannot be determined. Very few potentially useful taxonomic characters can, in fact, be discerned. On the carapace, only two pleurals separate the last neural from the suprapygal. There appears to be a deep indentation in the posterior edge of the pygal at the midline, and this, together with similar but not quite so pronounced indentations in the tenth and eleventh peripherals, gives the rear margin of the carapace a serrated appearance. Whereas the last vertebral was broader than long, the two preceding ones were longer than broad. The anal notch of the plastron is rather deep and narrow, and the lateral margins of the posterior lobe are sinuous. As a consequence, the xiphiplastral tips are much more elongate than in any other taxon yet described as a pelomedusid. Simpson (1943: 61) considered the deep anal notch and serrations along the posterior border of the carapace to be the species-specific characters of *P. geologorum,* and indeed, these are quite distinctive and indicate the validity of the species. Unfortunately, however,

[1] When Simpson described the type of *P. geologorum,* it was catalogued as AMNH 6781. It now belongs to the collections of the Museo de Ciencias Naturales, Caracas, and bears the number MCN 915.

on the basis of present evidence there is no reason to believe that *P. geologorum* is really a species of *Podocnemis* or, for that matter, of any pelomedusid. It cannot yet be confidently allocated to either of the two pleurodiran families to which it must belong, the Chelyidae or the Pelomedusidae. Thus, until better material of this taxon becomes available, *P. geologorum* should be listed as Pleurodira *incertae sedis*.

Three species of *Podocnemis* — *P. harrisi* (Pacheco, 1913), *P. brasiliensis* (Staesche, 1937)[1], and *P. elegans* (Suarez, 1969) — have been described from three widely separated localities within the Baurú Formation of southern Brazil. These sediments represent terrestrial deposition, with fluvial and alluvial plain beds predominating, and are probably of late Cretaceous (Senonian) age (Oliveira, 1956: 53–54). The only specimens ever referred to *P. harrisi* were a nearly complete right xiphiplastron and several peripherals (Pacheco, 1913: 37, pl. 3 [figs. 6a–e], pl. 4 [fig. 6]). Ischial and pubic scars on the visceral surface of the xiphiplastron clearly indicate that some kind of pleurodire is represented, but no other taxonomically useful evidence exists. It is therefore impossible to determine whether *P. harrisi* is a chelyid or a pelomedusid. Reference of this species to *Podocnemis* was unjustifiable, as Schmidt noted long ago (1931: 253). Furthermore, since the type material is now apparently lost (Price, 1953: 10), *"P. harrisi"* must be regarded as a *nomen vanum*.

On the basis of some photographs of a partial plastron, a carapace fragment[2], and three associated pleurals, Staesche (1937) described *P. brasiliensis*. The xiphiplastra of this species do not appear to differ in any appreciable way from those of *P. harrisi*, and therefore Simpson (1943: 61) may well have been correct in suggesting that *P. brasiliensis* is a synonym of *P. harrisi*, although Staesche (1937: 302–303) noted that his material differed in that it represented a somewhat larger individual with a different kind of sculpturing on the external surface of the shell, factors which might or might not be of taxonomic significance.

[1] Staesche (1944) is merely a translation of Staesche (1937) from German into Portuguese.

[2] This carapace fragment, together with a previously undescribed anterior lobe of a plastron from the same locality, was subsequently referred to a new genus and species, *Roxochelys wanderleyi*, by Price (1953).

Small, laterally placed mesoplastra were present, even though no longer preserved, so that *P. brasiliensis* is clearly a pelomedusid. An appropriate generic determination cannot at present be made, however, because much of the anterior plastral lobe, so critical for pelomedusid shell taxonomy, is missing. Thus, the specimen can neither be certainly referred to *Podocnemis* nor, owing it its imperfect preservation, can any species-specific characters be established. Until better material is available, therefore, the plastron and pleurals to which the name *P. brasiliensis* now applies should be designated as Pelomedusidae gen. et sp. indet. (*"Podocnemis brasiliensis"* Staesche).

Unlike the other two dubious "species" of *Podocnemis* from the Baurú Formation, *P. elegans* is clearly valid and referable to this genus. It is the only South American fossil pelomedusid yet described for which associated shells and skulls have been recovered. Furthermore, it is the oldest representative of *Podocnemis* known anywhere. It was described on the basis of two specimens, an essentially complete shell and a well-preserved skull belonging to a different individual[1]. A detailed description of this species will not be presented here since an account, based on additional new material as well as the original hypodigm, is being prepared by one of us (RCW) for separate publication. Some of the salient characters may be briefly noted, however. In most respects the shell is typical of all South American species of *Podocnemis,* but the shapes of the first two neurals are unique: instead of being spindle-shaped, the first is hexagonal, with the postero-lateral sides much shorter than the antero-lateral ones; and the second, rather than being hexagonal, is subrectangular. A unique feature of the skull is the total absence of triturating ridges on the palatal surface of the upper jaw. All other species have from one to three triturating ridges, the exact number being characteristic of different species. In addition, there does not seem to be an antero-posterior

[1] Suarez (1969: 37) stated: "Designamos como tipo da nova especie a carapaca e plastrão com craneo e diversos elementos esqueletais . . ." The shell and skeletal elements belong to one individual and there is in fact a badly crushed skull (which was not illustrated or discussed) associated with them, but it is not the skull described by Suarez. This is an isolated one from a much larger individual. Both specimens are in the paleontological collections of the Faculdade de Filosofia, Ciencias e Letras de Presidente Prudente; they bear no catalog numbers.

forehead groove between the orbits. Of the other South American species of *Podocnemis,* only *P. dumeriliana* lacks this groove. Perhaps the most extraordinary aspect of the skull of *P. elegans* is its modern appearance; archaic or ancestral features that one might expect to find in such an ancient species are notably lacking.

Cattoi and Freiberg (1958) described *Podocnemis argentinensis* from the Santa Barbara Formation[1] in the Province of Jujuy, Argentina. It is known from a large part of a plastron, lacking the terminal portions of the anterior and posterior lobes as well as much of the bridges, and most of the right epiplastron of a second individual. The systematic position of this form is uncertain. Laterally placed mesoplastra were definitely present, as evidenced by the semicircular excavations on either side of the plastron at the base of the bridge, so that *argentinensis* clearly represents some kind of pelomedusid. Too little of the shell has been preserved, however, to permit assignment to *Podocnemis* with any degree of confidence. At a lower taxonomic level, the characters used to define the species are in some cases questionable and in others of little or no taxonomic significance. Cattoi and Freiberg described the entoplastron as cordiform, but in their figure and plate it appears to be quadrangular. Examination of the specimen itself indicates that the entoplastron is slightly damaged anteriorly and that it was probably diamond-shaped originally. Small, triangular gular scutes are characteristic of most pelomedusids, but the relatively small intergular, which was probably pentagonal, is certainly reminiscent of the condition typical of South American species of *Podocnemis* and the North American *Bothremys* (Gaffney and Zangerl, 1968). The various scute proportions cited by Cattoi and Freiberg in their diagnosis yield no useful taxonomic information. Anastomosing vermiculations cover the external plastral surface as in the majority of pelomedusid

[1]Various ages have been assigned to this stratigraphic unit, formerly referred to as the Margas Multicolores. Cattoi and Freiberg placed it in the late Cretaceous, while Bardack (1961) considered it to be middle Tertiary. The recent discovery of a mammal skull high in the formation indicates a Paleocene or early Eocene age (R. Pascual, personal communication). There is some uncertainty as to whether these beds are of marine or terrestrial origin (Cattoi and Freiberg, 1958: 59).

genera[1]. Until better material becomes available, it will not be possible to determine the systematic position of this turtle. In the meantime, it must be referred to as Pelomedusidae gen. et sp. indet. (*"Podocnemis argentinensis"* Cattoi and Freiberg).

The type and only specimen of *Podocnemis bassleri* (Williams, 1956) is a large, exceedingly well-preserved skull. It was collected in eastern Peru from beds of the Contamana Group, which includes sediments believed to range in age from Eocene to possibly at late as Pliocene. Williams, on the basis of information supplied by Kummel, reported that the skull "came from the uppermost part of the . . . group," which suggests that its age falls within the latter part of the Tertiary. He further remarked that "The fossil itself is so close to a Recent species as to tend to support the latest date geologically permissible." The skull differs only in minor details from that of the living *P. expansa.* It seems fairly certain that *P. bassleri* was closely related, if not directly ancestral, to this species.

Unfortunately, the evolutionary history of *Podocnemis* in South America cannot be reconstructed on the basis of present information. Only three fossil species — *P. bassleri, P. elegans,* and *P. venezuelensis* — are of unquestionable validity. One of these, *P. bassleri,* is clearly very closely related to *P. expansa.* The relationships of the other two extinct species to living South American forms are uncertain, owing to their distinctive shell characters. With the exception of *P. lewyand*[2], the living South American species of *Podocnemis* are all strikingly similar in terms of shell

[1] Cattoi and Freiberg's figure 1 shows the entoplastron as being nearly encompassed by unusually large epiplastra, a condition unknown in any other chelonians that we are aware of. However, their sketch does not accurately represent the positions of the sutures between the epiplastra and hyoplastra; these are, in fact, disposed in typical pelomedusid fashion, extending outward from the lateral apices of the entoplastron.

[2] Through the courtesy of Professor F. Medem, one of us (RCW) has been able to examine a series of six *P. lewyana* shells in the collections of the Instituto Roberto Franco at Villavicencio, Colombia. None of these has a suprapygal bone on the carapace; instead, each of the last (eighth) pleurals is subtriangular, not trapezial as is the case in other species of the genus, and these pleurals are in continuous contact along the midline from the posterior end of the seventh pair of pleurals to the pygal.

morphology. Only small structural details characteristic of each taxon permit differentiation among them on the basis of shells alone. *P. venezuelensis* stands markedly apart from all other species of the genus in its total lack of neurals, and certainly could not have given rise to any of the living forms. Nothing remotely resembling the shapes of the first two neurals in *P. elegans* is encountered elsewhere in the genus. So conservative in structure is this part of the shell in all other species (except, of course, for *P. venezuelensis*), and so radically different is it in *P. elegans,* that this species could hardly have been ancestral to any or all of the later species known from South America. Thus, neither *P. elegans* nor *P. venezuelensis* has any obvious relationship to living species of the genus or to each other. A much better fossil record for *Podocnemis* will be necessary before a meaningful picture of its evolutionary history in South America can be formulated.

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We are particularly grateful to Señora Frances Charlton de Rivero, retired professor of paleontology at the Escuela de Geologia y Minas in Caracas, not only for her gracious hospitality but also for having provided laboratory facilities while the material here described was being studied. Both authors have examined the type specimen of *"Podocnemis" geologorum* and one of us (RCW) has also been able to examine the types of *"P. argentinensis," P. bassleri,* and *"P. brasiliensis."* We would like to thank the curators of the various institutions at which these fossils are housed for permission to study them. Through the kindness of Professor José Martin Suarez, RCW has not only been able to study the type material of *P. elegans* but also to visit the locality from which it was recovered. Without a generous grant to RCW from the National Geographic Society, none of this work would have been possible. We are much obliged to Professors F. Medem, B. Patterson, P. E. Vanzolini, and E. E. Williams, and to Dr. M. Freiberg for their comments and discussions on various aspects of this manuscript.

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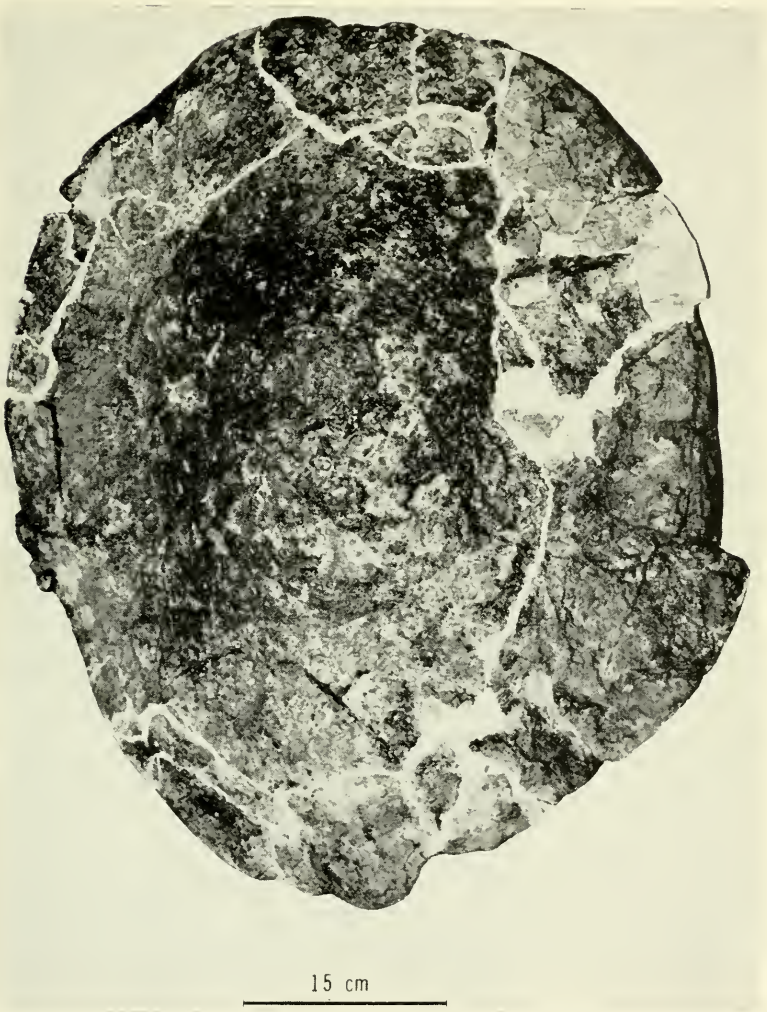

Plate I. Dorsal view of the type carapace (VF 1176) of *Podocnemis venezuelensis*.

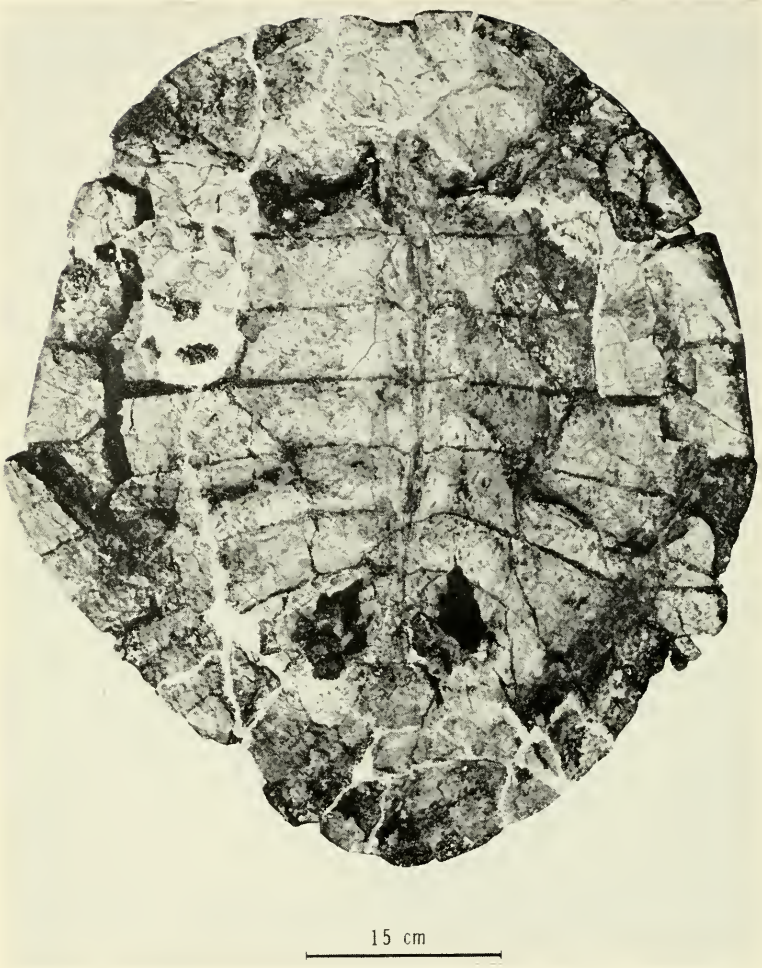

Plate II. View of the visceral surface of the type carapace (VF 1176) of *Podocnemis venezuelensis*. Note the absence of neural bones.

Plate III. View of the visceral surface of the type plastron of *Podocnemis venezuelensis* (VF 1173), showing the disposition of the pelvic attachments to it.

Plate IV. Ventral view of the type shell of *Podocnemis venezuelensis*, with the plastron (VF 1173) positioned correctly in relation to the carapace (VF 1176).

Plate V. The visceral surface of VF 1174, a partial plastron of *Podocnemis venezuelensis,* showing clearly the outlines of the laterally placed mesoplastra.

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA IX. THE CHANARES FORMATION

Alfred Sherwood Romer

ABSTRACT. The term "Chañares Formation" should be retained for the fossiliferous beds so named by Romer and Jensen; the type section of the "Ischichuca Formation" is homologous with part of the overlying Los Rastros Formation.

With the discovery of a rich Triassic reptilian fauna in the Chañares-Gualo region of La Rioja Province, Mr. James Jensen and I set about the task of determining the stratigraphic sequence of the area (Romer and Jensen, 1966). It was soon apparent that, despite complex faulting, a series of formations with clear-cut boundaries could be distinguished, and in the Arroyo del Agua Escondida the entire local series could be seen in proper sequence.

The area is part of a basin of late Paleozoic and early Mesozoic deposition lying in western La Rioja Province and an adjacent portion of San Juan, extending roughly from the western flanks of the Sañogasta Range on the east to the Río Bermejo on the west, and from the region of Villa Unión south to the northern end of the Valle Fertil range. The center of this area is the flat Campo de Talampaya, and I shall term this cuenca the Talampaya Basin. Little attention had ever been given to the geology of our area of interest in the eastern part of the basin, but considerable work had been done in the western part. It was obvious that the thickness and nature of the sediments varied greatly from one basin area to another, and the situation was further complicated by the fact that there had been much volcanic activity. As far as possible we utilized formation names already in the literature; when no similarities to named formations in other areas in the basin were discernible, new names were given. The formations named by us are shown in the right hand column of the table. The

three formations latest in time — Los Colorados, Ischigualasto[1] and Los Rastros — are comparable to those so named to the west, across the Campo de Talampaya, although much thinner in our area in each instance. Below the normal beds of the Los Rastros, strongly carbonaceous in nature, are some 70 meters of evenly bedded volcanic ash sediments in which fossil reptiles are abundant. Despite the fact that these strata are quite conformable with the overlying Los Rastros deposits, they are, as layers of white to bluish white ash, quite distinctive in character and, since they are the bearers of our fauna, we ventured to separate them from the Los Rastros as a distinct Chañares Formation. Below them, unconformably, are red and white sandstones which are roughly comparable to those generally assigned to "Paganzo III." Since this is not a proper stratigraphic term, we have given them the name of the Tarjados Formation. Beneath them, again, are thick series of soft sandstones, perhaps also part of the "Paganzo III" complex, for which we have found no clear equivalents in other parts of the basin, and which we have named the Talampaya Formation.

In general, I think, this terminology has been accepted. The one exception is that Sr. Bonaparte (1967, 1969, etc.) has objected to our term "Chañares Formation," and maintains that these beds should bear the name "Ischichuca Formation." Despite the high regard I have for Sr. Bonaparte's work in the collection and description of Triassic fossils, I believe that this usage is indefensible. A review of the history of stratigraphic work in this region is necessary.

The first serious study of this region was that of Bodenbender (1911). His stratigraphic section in this basin is given in the first column of the table. He believed that the sediments in this area extended from the Carboniferous to the Cretaceous, and for the lower beds in the region invented the term "Paganzo," divided into "Paganzo I" for light colored sediments which he believed (apparently correctly) to be of Carboniferous age, "Paganzo II," for red sandstones which (again probably correctly) he thought were Permian, and "Paganzo III," for beds, mainly reddish sandstones, which (with less assurance) he claimed to be Triassic.

[1] Sr. R. R. de la Vega has pointed out to me that the correct spelling should be Ichigualasto, but the "improper" version has become so embedded in the literature that it seems impossible to eradicate it.

"Rhaetic" was a favorite term with early German workers in South American geology, favored perhaps because of its rather vague meaning, and to the "Rhaetic" he assigned a very considerable thickness of beds including yellow and variegated shales, coal shales, and coal seams. Above these (beyond some indeterminate beds in the region of Cerro Morado, which he suggested were possibly Jurassic) the depositional series terminated with thick red sandstones which he believed to be Cretaceous in age and termed the "Cretáceo Andino."

A more thorough study of the beds of the western part of the basin was undertaken in the 1940's by Frenguelli and by de la Mota. Frenguelli mainly visited the region of the Ischigualasto Valley, drained to the west by the Río de la Peña, and published his results in 1948. Bodenbender's "Cretáceo Andino" beds were termed by him the "Estratos de Gualo," and their presumed age reduced, reasonably, from Cretaceous to "Rhaetic." In Bodenbender's erstwhile "Rhaetic" series he distinguished an upper member as the Ischigualasto Formation — a series of variegated shales and some sandstones characteristic of the Ischigualasto Valley west of the red bluffs of the "Gualo." These beds are now known to possess a very considerable fauna of Triassic (? Ladinian or possibly Carnian) age. Below the Ischigualasto, to the west, and traversed by the difficult gorge of the La Peña, are rugged hills of sandstones and shales including coal seams, in which footprints had been discovered (Huene, 1931). As Frenguelli notes (1948: 191), he did not penetrate much farther to the west through the rugged country in the Ischigualasto-La Peña region than the Quebrada de los Rastros, where a coal mine is located and where the footprints were found; some data were furnished him by Ramaccioni and Heim, who studied the coal beds (Heim, 1949). They informed him that these "Rhaetic" beds were underlain, to the west, by red "Paganzo" sandstones which he cites as "Paganzo II" (they are actually of "Paganzo III" age).

The total thickness of the "Rhaetic" beds below the Ischigualasto Formation in this region was estimated as 600–650 meters. Frenguelli made this area the type section of the Los Rastros Formation, to which he assigned the upper 400–450 meters of these beds — i.e., about two-thirds, on his reckoning. As can be seen from the sections of Ortíz, mentioned later, under this definition of the Los Rastros the formation would include essentially

the whole of the coal-bearing portion of the "Rhaetic" beds. In default of personal knowledge of the lower beds in the Ischigualasto-La Peña region, Frenguelli turned to the region of Cerro Bola, some 70 km to the north, which had been studied in detail by de la Mota (whose results are recorded in an unpublished thesis at the University of La Plata).[1] Equivalents of the "Gualo" and Ischigualasto beds are readily determinable in the Cerro Bola region. Between the Ischigualasto and "Paganzo III" there are here, much as in the Ischigualasto region, some 500–550 meters of "Rhaetic" beds of sandstones, shales, and coal seams. The upper 250–300 meters of these beds were equated by de la Mota and Frenguelli with the type Los Rastros; they contain occasional carbonaceous seams, but consist mainly of shales and fine-grained olive-green sands. The beds below, with a thickness of about 250 meters, are here the main coal-bearing strata, dominantly black or grey-black in color, with some intercalations of thin olive-green sands. These beds were named the Ischichuca Formation, the type section being located in the quebrada of that name south of Cerro Bola. Below the Ischichuca Formation lies "Paganzo III." This consists mainly of coarse red sandstone and intercalated volcanic beds; between the beds of "Paganzo III" proper and the Ischichuca are 30–40 meters of coarse grey to reddish conglomerates which de la Mota assigned to "Paganzo III."

Frenguelli's sections of the basin, derived from two areas 70 km apart, are given in the second and third columns of our table. In 1953 Groeber and Stipanicic (pp. 87–93), in their review of the Triassic, followed Frenguelli, as given in our column 4, except that his "Estratos de Gualo" are renamed "Estratos de los Colorados," (since de la Mota had pointed out to them that the Mogote del Gualo lies at a much lower stratigraphic position than Frenguelli believed).

A decade later than the visit of Frenguelli to the Talampaya Basin, study of the region to the west of Ischigualasto, down the La Peña, was undertaken by Ortíz on behalf of the Yacimientos Petrolíferos Fiscales. His work was done in 1964, and his sections and maps were promptly circulated, although publication of his work was not made until 1968. As his sections show, the actual

[1] Resumés of de la Mota's findings are given by Frenguelli (1948: 197–208) and by Groeber and Stipanicic (1953: 93–95).

sequence of the "Rhaetic" beds here, below the Ischigualasto, differs considerably from that imagined by Frenguelli and studied by him in the Cerro Bola region, and the strata are considerably thicker than had been believed. The upper part of the type Los Rastros Formation, to about 250 meters, consists mainly of grey sandstones with intervening shales and only a few coal seams. Below this, but also included by Frenguelli — entirely or at least for their most part — in the type section of the Los Rastros Formation are about 400 meters of beds in which dark carbonaceous shales and coal seams predominate, with intervals of olive-green shales. Below the coal beds, again, are about 450 meters of conglomeratic sandstones, light in color, in which coals are little developed. Still farther down to the west appear the red sandstones of "Paganzo III."

It is clear that Frenguelli's nomenclature of the Los Rastros and Ischichuca beds in the two regions, that of the La Peña and the Ischichuca quebrada, is conflicting. The beds assigned to the Los Rastros in the Ischichuca region include only the upper part of the type Los Rastros; the middle, coal-bearing section of the beds which were included in the type Los Rastros in the La Peña region, form to the north practically the entire Ischichuca Formation. The lowest portion of the "Rhaetic" beds in the La Peña area has no counterpart in the north, unless it be the thin series of conglomerates that were mentioned above as transitional from "Paganzo III" to Ischichuca. As Ortiz points out, the entire series of beds from "Paganzo III" up to the Ischigualasto forms a single cycle of deposition, to the whole of which the formation name Los Rastros should properly be applied. Further, since the supposed Ischichuca Formation is merely a portion of the Los Rastros — the lower portion by Frenguelli's definition, the middle portion under Ortíz's suggestion — the term "Ischichuca" should be abandoned, as simply a partial synonym of Los Rastros.

The Triassic sequence in the Talampaya-Ischigualasto basin as interpreted by Ortíz is given in column 5 of our table. Our own interpretation, given in column 7 and mentioned earlier, is in most regards comparable. The identity of the Los Colorados and Ischigualasto formations is perfectly clear; we have given names, as the Tarjados and Talampaya formations, to the red sandstones and underlying finer sandstone beds that have previously been referred to under the vague generic term "Paganzo III." We have, with Ortíz, agreed that the coal-bearing sandstones and shales of

the "Rhactic" should be considered as a single Los Rastros Formation rather than be subdivided in two in a confusing fashion. Our one difference has been in distinguishing the lowest part of this cycle as a separate Chañares Formation because of its distinctive nature and, especially, because of the paleontological importance of this unit.

Bonaparte, independently of Ortíz, studied the lower western portion of the beds which Ortíz has described and, like Ortíz and in contrast to Frenguelli's hypothetical interpretation, finds that the lower part of the Los Rastros complex consists of light colored shales without coal seams, and thus is somewhat comparable to our Chañares beds. He is, further, to be congratulated for finding in them fossils which are presumably comparable to those from the Chañares. Quite probably the lowest section of the Los Rastros of Ortíz and the Chañares beds are homologous (although the Los Rastros beds contain conglomerates, quite in contrast with the even bedding of the Chañares). How should the matter be treated? It may be advocated either that the Chañares be considered as a lower member of the Los Rastros or that the lower segment of the Los Rastros in the La Peña area be considered as a separate Chañares Formation.

Bonaparte, however, would go further and revive the term "Ischichuca" for these beds. Essentially, his argument is that since these beds in the La Peña region were termed Ischichuca by Frenguelli (who had never seen them and was ignorant of their nature), the name should be retained. To so argue, however, is to violate the basic principles of stratigraphic nomenclature. One should refer to the type section of the Ischichuca, 70 km to the north. The type Ischichuca consists of the main coal-bearing section of the "Rhaetic." As Ortíz has shown, the supposed "Ischichuca" in the La Peña region is at a higher stratigraphic level than the beds with which we are concerned and is, by Frenguelli's definition, equivalent to part of the Los Rastros. No two sets of beds could differ more in nature than the blackish "coal measures" of the Ischichuca and the clear white ash of the Chañares. Both the nature of the beds and their stratigraphic position distinguish clearly the type "Ischichuca" from the lower Los Rastros and Chañares beds. The use of "Ischichuca" for the latter strata cannot be defended.

<table>
<tr><td rowspan="2">Bodenbender
1911</td><td colspan="2" rowspan="2">Frenguelli
1948</td><td rowspan="2">Groeber &
Stipanicic
1953</td><td rowspan="2">Ortíz
1964, 1968</td><td rowspan="2">Bonaparte
1967, 1969</td><td rowspan="2">Romer &
Jensen
1966</td></tr>
<tr></tr>
<tr><td>Cretácea
Andino</td><td colspan="2">Gualo</td><td colspan="4">Los Colorados</td></tr>
<tr><td rowspan="4">Rhaetic</td><td colspan="6">Ischigualasto</td></tr>
<tr><td>Los Rastros</td><td rowspan="2">Los Rastros type locality</td><td rowspan="3">Los
Rastros</td><td colspan="2" rowspan="2">Los Rastros</td></tr>
<tr><td rowspan="2">Ischichuca
type locality</td></tr>
<tr><td>Ischichuca</td></tr>
<tr><td colspan="3" rowspan="2">Paganzo III</td><td>Ischichuca</td><td>Chañares</td></tr>
<tr><td colspan="2" rowspan="2">Paganzo III</td><td>Tarjados</td></tr>
<tr><td colspan="3">Talampaya</td></tr>
</table>

Table to show various interpretations of the Triassic sequence in the Talampaya Basin.

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BREVIORA

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA

X. TWO NEW BUT INCOMPLETELY KNOWN LONG-LIMBED PSEUDOSUCHIANS.

Alfred Sherwood Romer

ABSTRACT. Two types of hind limbs, with which incomplete remains of other skeletal parts are associated, are described as new genera and species, *Lagerpeton chanarensis* and *Lagosuchus talampayensis*. Both have long and slender legs, with the tibia longer than the femur, and a long slender foot. They differ, however, in foot construction, for in *Lagerpeton* digit II is short and digit IV the longest of the series, whereas in *Lagosuchus* metatarsals II–IV are subequal in length and digit III the longest in the foot.

INTRODUCTION

In the pseudosuchian material collected by the La Plata-Harvard expedition of 1964–1965, there are several forms represented by nearly complete skeletal material. In addition, however, in this collection and among specimens collected later by Sr. Bonaparte of the Instituto Lillo of Tucumán, there are less complete remains of further pseudosuchians. Two such forms are represented by materials including hind limbs of unusual and advanced character; these will be described here.

LAGERPETON CHANARENSIS gen. et sp. nov.

Holotype. La Plata Museum No. 64–XI–14–10 (field number 64), a hind leg, collected from the Chañares Formation in La Rioja Province, Argentina, about 4½ miles east of the mouth of Río Chañares.

Combined generic and specific diagnosis. A pseudosuchian; hind limb very long and slender; femur with articular head sharply set off from shaft; tibia and fibula longer than femur; astragalus

and calcaneum fused and applied closely to tibia and fibula; toe IV longest of the hind leg digits; toe II much shorter than III or IV; toe V represented by short metatarsal only.

Description. The type specimen (Fig. 1) was found quite isolated, not articulated with or accompanied by other skeletal materials. The femur is long and slender, with a length of 77 mm. It has the typical sigmoidal archosaur shape. The well-ossified curved articular area of the head is pronounced and set off at a sharp angle from the shaft. A marked angulation of the posterior

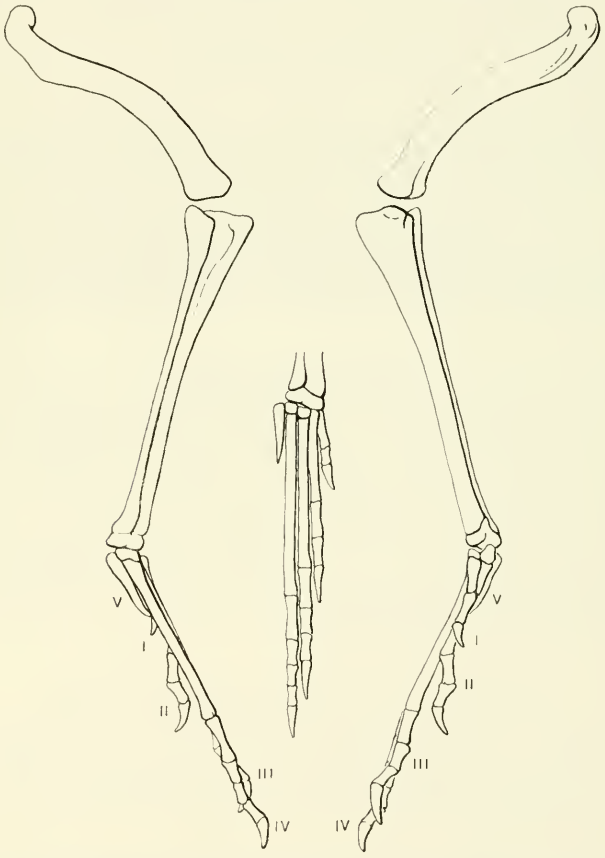

Figure 1. Right hind leg of *Lagerpeton,* holotype. Left, external view; center, extensor surface of foot; right, internal view. × 1/2.

margin of the shaft indicates the point of insertion of musculature, presumably the iliofemoralis. On the medial surface below the head, there is a well-developed fourth trochanter in the shape of a pronounced ridge, presumably for the insertion of the caudifemoralis.

The epipodials are even more elongate and slender than the femur; the tibia measures 92 mm in length, and is thus about 120 per cent the length of the femur. The tibia is well expanded proximally for a broad double articulation with the distal end of the femur. The fibula is incomplete in the type, and I have in my figure restored the proximal end from a specimen, discussed below, in the Instituto Lillo collection. It is, as always, a slender strap of bone expanded at either end; proximally, it articulates with the lateral surface of the distal end of the femur.

The proximal tarsals are of unusual construction for a thecodont. Astragalus and calcaneum are completely fused in the type specimen; in their combined outline they conform to the area of the distal end of tibia plus fibula, and this astragalo-calcaneum is closely applied to these two elements, although not fused with them. Further contributing to the close union of the astragalo-calcaneum with the epipodials is a triangular flange of bone extending upward from this element posteriorly over the lower ends of tibia and fibula. There is here no indication of the crocodiloid calcaneal tuber frequently found in pseudosuchians.

The usual two distal tarsals are present. A more medial and larger element is present on the ventral surface, above the third metatarsal; the lateral element caps metatarsal IV.

Like the main limb elements, the foot is long and slender, the toes apparently lying close together in life. Toe V is represented only by a short, pointed metapodial; the other toes are complete, with the primitive phalangeal formula of 2, 3, 4, 5. The terminal phalanges of toes I–IV are sharp claws, somewhat curved. Most unusual for an archosaur, the toes are primitive in one regard, namely that toe IV is the longest of the series. Digit I is, as often, short; digit II is also shortened, its metapodial having but about half the length of those of its lateral neighbors. The total lengths of the digits, from toe I outward, are 21, 49, 69, 85, and 18 mm. Metapodial lengths are 8, 24, 45, 48, and 18 mm.

In the Instituto Lillo collections is a specimen that includes a hind leg similar to that of the type in size, bone proportions, and

structure. The femur is 75 mm in length, the tibia (not perfectly preserved) about 90 mm. The femur is closely comparable to that of the type with its sharply set off head and prominent trochanteric ridge. Toe I is not preserved, but toes II–IV resemble closely those of the type, with metapodial lengths of 23, 42, and 47 mm, and total toe lengths of 48, 74, and 87 mm.

With this specimen is a pelvis which is apparently nearly complete, but in its present state of preparation is seen only from its ventral aspect. The ischia are well developed and extend far backward with a long symphysis. Below and somewhat to the rear of the level of the acetabulum their broad external surfaces are convex in section, giving this region a "swollen" appearance.

Lagosuchus talampayensis gen. et sp. nov.

Holotype. La Plata Museum No. 64–XI–14–11 (in part). Remains included in a slab collected from the Chañares Formation in La Rioja Province, Argentina, about 2 km north of the mouth of Río Chañares.

Combined generic and specific diagnosis. A pseudosuchian; hind limb similar in many regards to that of *Lagerpeton;* limb long and slender; femur with articular head sharply set off from shaft; tibia and fibula longer than femur; astragalus and calcaneum fused and applied closely to tibia and fibula. Digit I short, digit V represented by short metatarsal only; digits II–IV subequal in metatarsal length, but digit III longest of the series.

Description. A slab from the Chañares exhibits on one surface the greater part of the skeleton of a small ornithosuchid which I hope to describe in a later number of this series. On the other surface of the slab are scattered materials pertaining to a still smaller pseudosuchian. Best preserved are nearly complete and articulated hind limbs (Fig. 2). Although considerably smaller, these limbs in their proportions resemble those of *Lagerpeton,* and I at first assumed that the specimen was an immature individual of that genus. The foot structure, however, shows that we are dealing with a discrete form of smaller size.

As in *Lagerpeton,* the limbs are long and slender; the head of the femur is set off sharply from the shaft and the trochanteric ridge is well developed. As in *Lagerpeton* the lower leg is longer than the femur, the two femora, as preserved, having lengths of 38 and 39 mm, the associated tibiae 47 and approximately 48 mm.

Figure 2. Hind foot of *Lagosuchus,* in ventral view. Composite of type and a specimen in the Instituto Lillo. 1 1/2 × size of holotype.

The proximal tarsal region is poorly preserved in the type. Two well-developed distal tarsals are present. Of the right foot, only metapodials, incomplete distally, are visible. The left foot is well preserved as regards the metatarsals and a portion of the phalanges. The digits are elongate and slender; metapodials II–IV are, as preserved, parallel to one another and closely apposed. Digit I, with a metapodial length of 15 mm, is short; metapodials II–IV have lengths of 23, 26, and 25 mm; metapodial V, broad at its head, tapers, as preserved, to a point at 11 mm. The two phalanges appropriate to digit I are present, as are single proximal phalanges articulated with metatarsals II and III, and several disarticulated phalanges (one a clawed ungual).

Scattered about the slab are disconnected series of vertebrae with average lengths of centra of 7.5 mm in the best preserved

region. There are, further, remains of pectoral limbs. In the better preserved of these the humerus has a length of 26 mm, the radius 16 mm. As one might expect from the nature of the long hind legs, the front limbs thus appear to be much reduced in size, the combined length of the long bones of the "arm" being less than half that of the corresponding hind leg elements.

A specimen in the Instituto Lillo collection includes much of the posterior part of a skeleton that is closely comparable to the type of *Lagosuchus* except for somewhat larger size. Much of both hind legs is preserved in articulation. Right and left femora measure 55 and 56 mm in length, the tibiae 72 and 70 mm.

As in *Lagerpeton,* astragalus and calcaneum are united and closely applied to tibia and fibula. Here, however, the line of suture between the two proximal tarsals is still visible, and a small spur of bone (not seen in *Lagerpeton*) projects backward from the fibular edge of the astragalo-calcaneum. There is no proximal extension of the astragalo-calcaneum of the sort seen in *Lagerpeton.* The two distal tarsals are present lying above the metatarsal heads.

The feet are incompletely preserved, but except for somewhat larger size, they compare well with those of the type. On the right foot metatarsals II and IV have lengths of 34 and 38 mm, respectively; lengths of metatarsals I–IV on the left foot are: 23, 35, 39, and 38 mm. No phalanges are present on metatarsal I, but two phalanges, with lengths of 9 and 7 mm are present on the second digit, three phalanges with lengths of 12, 8, and 5 mm on digit III, and four phalanges with lengths of 6, 5, 4, and 4 mm on digit IV. Metatarsal V, broad at the base and tapering distally, is incomplete, with a length as preserved of 10 mm.

In Figure 2 the foot is restored as a composite of the type and the Instituto Lillo specimen just described, with allowance made for the difference in size of the two specimens. The more distal phalanges are restored on digits II–IV. As restored, digital lengths of the Instituto Lillo specimen are, from digit I outward: 36, 56, 69, and 62 mm. Here, in contrast to *Lagerpeton,* there has developed the "typical" archosaur foot, with toe I relatively short, toe V reduced, and toe III the longest of the II–III–IV series.

Associated are remains of the pelvic girdle. The acetabula (into which the femoral heads were inserted when the specimen was recovered) are small and deep, strongly overhung dorsally by

the iliac rim. The acetabular construction plus the nature of the femoral head indicate rather surely that the femur moved in a fore-and-aft plane close to the body. The ilium (Fig. 3) is of peculiar structure. Above the acetabulum it constricts to a relatively narrow neck. Here there projects anterolaterally a short but stout, blunt-ended process of a sort otherwise unknown to me; it is possible that it afforded an origin for an iliofemoralis externus muscle as in the case of a somewhat similar process in some ornithischians (cf. Romer, 1927) and *Poposaurus* (Colbert,

Figure 3. Right ilium and head of femur of *Lagosuchus;* external process on ilium restored from left side. From a specimen in the Instituto Lillo. × 4/3.

1961). Above the "neck," the ilium expands to form a short blade. In all "normal" thecodonts the iliac blade is a simple single vertical structure; here, however, there lies, internal to the normal external blade, a broad trough, comparable to that seen in ophiacodonts, presumably for accommodation of dorsal axial muscles. Shallow posteriorly, this trough deepens and broadens anteriorly. Medial to this trough is a second iliac blade, tilted somewhat medially, to the inner surface of which the sacral ribs presumably articulated. Lateral and medial blades join anteriorly, closing the dorsal trough at this end. I know of such an iliac "trough" structure in only one other archosaur. In *Hesperosuchus,* Colbert (1952) found in the pelvic region an element which should have been an ilium but which, because of its peculiar nature, he concluded could not be that element. Its main peculiarity is its possession of a dorsal "trough" comparable to that of *Lagosuchus.*

Parts of pubis and ischium are present in this specimen. It is

clear that both pubis and ischium take part in the acetabulum, but in default of a better preserved specimen I refrain from discussion of this portion of the girdle.

Found close to the limbs and pelvic remains were two series of vertebrae. One appears to include sacrals, followed by nine proximal caudals. The mean length of these caudal centra is approximately 7 mm. A first chevron is present between caudals three and four; its length is 13.5 mm; those following decrease in length, the fourth of the series measuring 10 mm. A second series of vertebrae includes 30 segments, apparently running to the tip of the tail. The first dozen, poorly preserved, appear to have a mean length of centra of about 7 mm; more posteriorly, the length increases to about 1 cm per segment. Chevrons, gradually decreasing in length to a nubbin, are present, as preserved, to a position between the tenth and eleventh from the end of the series.

A further Instituto Lillo specimen that may pertain to *Lagosuchus* includes an imperfect pelvis and much of the hind legs. As in both genera described in the present paper, the tibia is longer than the femur, with measurements of the right leg elements of 48 and 42 mm, respectively. As in *Lagosuchus,* metatarsals II–IV are subequal in length, with measurements of 24, 28, and 27 mm for these metapodials in the left foot. Possibly associated is a fragment of maxilla or dentary bearing small teeth spaced a bit more than a millimeter apart. A number of posterior dorsal vertebrae are present, with an average central length of 5.5 mm and a height of 7.5 to 8 mm.

DISCUSSION

So distinctive are the hind legs which are the major preserved portions of the two forms described above that formal systematic description of them seems justified despite the paucity of further associated anatomical structures. Greater length of tibia than of femur is generally regarded as associated with speed. Greater length of lower leg than thigh is present in relatively few cases among even presumably bipedal archosaurs — a few thecodonts, such as *Scleromochlus,* small coelurosaurs, and to a slight degree in some carnosaurs. The sharply inturned head of the femur indicates that the hind legs were carried close to and beneath the trunk and the suggestion that we are dealing with a biped is increased by the shortness of the front legs of *Lagosuchus.*

It is surprising to find so advanced a type of limb at such an early stage of the Triassic (probably Anisian in terms of the marine series). In the preceding *Cynognathus* stage of the "Eotriassic," thecodonts more advanced than proterosuchians such as *Chasmatosaurus* and *Erythrosuchus* were represented only by *Euparkeria,* as recently ably described by Ewer (1965). *Euparkeria* was advancing toward a bipedal habitus, but was still relatively primitive. One would have expected that, in the Anisian, pseudosuchians would not have advanced far beyond this level, and that forms with limbs of such an advanced sort as seen in the two types just discussed should have been characteristic only of a much later stage of the Triassic. Obviously, as these forms indicate, this assumption is incorrect. It would seem that advance and radiation among thecodonts occurred rapidly in early Triassic times; beliefs to the contrary were due to our lack of knowledge of middle Triassic faunas; study of South American forms is now bringing such faunas into the picture.

As was first clearly brought out by Krebs (1963), two distinct types of tarsal joints developed among thecodonts. In one, retained by crocodilians, the main joint between lower leg and foot lay between astragalus and calcaneum. The second type of joint is that found in dinosaurs, in which the proximal tarsals were functionally combined with the lower leg, the distal tarsals united with the foot. Both forms here described are of the second type. However, the presence of a small spur on the calcaneal region of *Lagosuchus* suggests the possibility that a transition from one type to the other may have been possible. Fusion of the two proximal elements is a condition rare even in "advanced" dinosaurs. The development of a proximal flange from the astragalo-calcaneum, seen in *Lagerpeton,* is a condition found in various theropods, but in these forms the flange is developed on the extensor rather than the flexor surface of the lower leg.

With the marked expansion of our knowledge of thecodonts that is currently taking place, classification of the group can be at best but a provisional matter, and an attempt to place the two genera just discussed in a "solid" systematic position is unjustified. It is certain that the two have no association with the series of forms which appear to have crocodilian relationships, and the tarsal construction suggests that the two are connected in some fashion with a radiation leading toward the dinosaurs and, particularly, toward the coelurosaurian group of the Saurischia.

Whether either of the two, however, can be regarded as close to the direct line leading to such dinosaurs is doubtful. *Lagerpeton* is, on the one hand, advanced in tarsal construction and, on the other, primitive or specialized in the matter of relative length of digit IV. *Lagosuchus* is more orthodox in digital construction, but precocious in astragalo-calcanear fusion, and specialized in iliac construction.

There is a classic story of the man who "mounted his horse and galloped off in all directions." The history of thecodonts, we are coming to realize, seems to have followed this pattern. We have as yet no clues as to the course followed toward birds or pterosaurs. Various thecodonts seem to have trended toward a crocodilian type of organization. The ornithischian pattern is so distinctive that at the present we can reasonably consider the Ornithischia as definitely monophyletic in origin. This is not the case with the Saurischia. The presence in the later Triassic of apparent sauropod ancestors of seemingly primitive quadrupedal nature suggests a polyphyletic origin of that order. What of the "prosauropods" of the late Triassic, the coelurosaurs, the advanced theropods of the Jurassic and Cretaceous? Quite possibly the Saurischia are a polyphyletic group that took origin from a "mixed grill" of thecodonts — a varied assemblage amongst which the two forms here described are to be included.

I am indebted to the National Science Foundation, grants GB-2454 and GB-8171, for aid in the collection, preparation, and publication of the La Plata-Harvard materials, and I am grateful to Sr. Bonaparte for the privilege of studying the Chañares thecodont material which he has collected.

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA XI. TWO NEW LONG-SNOUTED THECODONTS, *CHANARESUCHUS* AND *GUALOSUCHUS*

Alfred Sherwood Romer

ABSTRACT. A description is given of the skull and jaws of two new thecodonts, *Chanaresuchus bonapartei* and *Gualosuchus reigi,* from the early Middle Triassic Chañares Formation of Argentina. The two forms here described plus *Cerritosaurus* and *Proterochampsa* are closely related and may be included in the single family Proterochampsidae. Their structure is in many regards so primitive that this family should be included in the thecodont suborder Proterosuchia. Suggested relationships of members of the family to crocodilians and phytosaurs are discussed.

INTRODUCTION

Commonest of all thecodont remains so far discovered in the Chañares Formation are those of *Chanaresuchus bonapartei* and *Gualosuchus reigi.* Considerable material, particularly of *Chanaresuchus,* was found by the La Plata-Harvard expedition of 1964–65, and further specimens, which Sr. Bonaparte has been kind enough to let me study, are in the collections of the Instituto Lillo of Tucumán. In the present paper I will confine myself to description of the skulls and jaws of these two closely related forms; I hope shortly to give an account of the postcranial skeleton of *Chanaresuchus.*

I gratefully acknowledge grants from the National Science Foundation that covered most of the expenses of collection and preparation of the materials, and for aid in publication.

CHANARESUCHUS BONAPARTEI, gen. et sp. nov.

Holotype. La Plata Museum 1964–XI–14–12 (field no. 47), a skull and jaws together with postcranial remains. Collected

from the Chañares Formation, in La Rioja Province, about half a mile southeast of a volcanic plug in the valley of the south fork of the Chañares River.

Combined generic and specific characters. A thecodont of modest size (largest known skull about 260 mm in length). Skull long and low; broad posteriorly; slitlike external nares placed close together dorsally some distance back of tip of snout; antorbital vacuity small; postfrontal absent; no pineal opening; parietals swing sharply outward posteriorly, above superior temporal fenestrae, toward meeting with squamosals; suspensorium far back of occiput, and lateral fenestra hence elongate anteroposteriorly. Very elongate choanae partially covered below by a secondary palate. Pterygoid and palatine toothed. Basal articulation of braincase and palate movable. A long if narrow interpterygoid vacuity, exposing a slender parasphenoid rostrum.

The generic name refers to the Chañares River and Formation. The specific name is given in honor of Sr. José Bonaparte, able collector and describer of Triassic reptiles.

Description (Figs. 1–3). Considerable skull material of *Chanaresuchus* is available. Most notable in the La Plata-Harvard collection, in addition to the holotype, are MCZ 4037 (field no. 154), which includes a large skull and jaws, and MCZ 4039 (field no. 81), the well-preserved left half of a small skull. Skull lengths of these three specimens (measured to the quadrate) are, respectively, 211 mm, 260 mm, and 155 mm. MCZ 4036 consists of a slab containing, as well as considerable postcranial material, two rather poor skulls of about the size of the holotype.

The dermal bones of the skull are ornamented, particularly on the skull table, with ridges radiating from centers of ossification. The degree of sculpturing appears to vary with size and presumed age; it is little developed on MCZ 4039, somewhat more prominent on the type, and the largest skull, MCZ 4037, is quite rugose.

The skull is long, low, slender-snouted, broad posteriorly. Snout elongation is clearly shown by the length of premaxillae, nasals, and frontals, and by proportionate measurements. If, for example, the anteroposterior diameter of the orbit be taken as a base, the facial length, anterior to the orbit, is about 4½ times the length of the orbit itself, whereas in other thecodonts

(phytosaurs excepted) this measurement is typically no more than two or three times the orbital diameter. There is, further, a considerable degree of postorbital length. From the postorbital bar to the tip of the quadrate, the distance is about 2½ times the orbital diameter, whereas in pseudosuchians this distance is almost invariably considerably less, and is sometimes not even equal to orbital diameter. It is difficult to select a standard against which skull height may be objectively measured, but it may be noted that even in the postfacial region of the skull, where flattening is less pronounced than in the snout, the skull height is not sufficient to give space for the eyes in the lateral wall and the orbits are, in consequence, incised into the skull roof.

The tip of the snout is slightly decurved. Dorsal and lateral surfaces of the skull are clearly marked off from one another. The dorsal surface is nearly flat, although rising along the length of the snout to then become horizontal in plane along the length of the skull table. On either side a well-marked ridge, separating lateral and dorsal surfaces, develops at the level of the nares and continues back to the anterodorsal angle of the orbit, where there is a modestly developed lateral projection. A similar projecting angle is present at the posterior margin of the orbit, and a clear-cut angle separating roof from "cheek" continues along the bar separating the temporal fenestrae.

The external nares are elongate slitlike structures, dorsally placed and close together, separated only by a narrow bony bar. In contrast to the subterminal position seen in many thecodonts, they are placed well back of the snout tip; grooves leading into the narial openings are present anteriorly and posteriorly. Deep to the external nares, and separated from the narial margins at all points, is seen a sheet of bone within which is found, on either side, an opening of considerably smaller size than the narial opening. At first glance one would assume that these openings are the choanae; however, as discussed below, they are apparently anterior palatal foramina for the vomeronasal organs, and this bony sheet forms a short secondary palate. This secondary palate is separated from the bone rimming the narial margin for only a short distance on the anterior and lateral margins; medially, however, the bony sheets of the two sides appear to meet one another below and free from the bar separating the two nares, and the opening posteriorly between the

narial margin and the secondary palate leads into a short naso-palatine duct.

The antorbital fenestra is a small triangular opening, the apex of the triangle lying anteriorly, at about one-third the distance from orbit to snout tip, the posterior base separated from the orbit by a narrow bony bar. The orbits are large (as, presumably were the eyes) and are subcircular in shape; on the lateral surface they occupy nearly the whole height of the skull, leaving but a narrow bar of bone between them and the lower skull margin. Dorsally their semicircular margins cut far into the sides of the skull table. The upper rim is slightly elevated; as mentioned, there are pronounced projections anteriorly and posteriorly at the junction of dorsal and lateral portions of the orbital boundaries.

There is no parietal foramen. The superior temporal fenestra is well developed, facing directly dorsally, and is triangular in

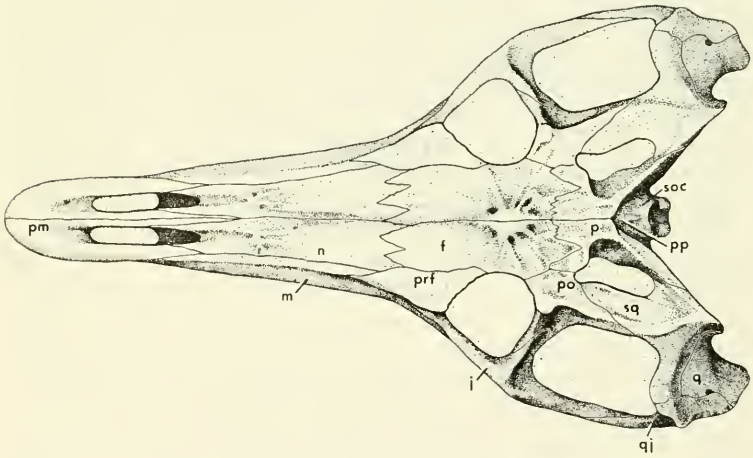

Figure 1. *Chanaresuchus bonapartei,* skull in dorsal view. This and Figs. 2–5 are based on the holotype, with additions from other specimens. Abbreviations for Figs. 1–7: *an,* angular; *ar,* articular; *bo,* basioccipital; *c,* coronoid; *d,* dentary; *ec,* ectopterygoid; *f,* frontal; *j,* jugal; *l,* lacrimal; *m,* maxilla; *n,* nasal; *op,* opisthotic; *p,* parietal; *part,* prearticular; *pl,* palatine; *pm,* premaxilla; *po,* postorbital; *pp,* postparietal; *prf,* prefrontal; *ps,* parasphenoid; *pt,* pterygoid; *q,* quadrate; *qj,* quadratojugal; *san,* surangular; *soc,* supraoccipital; *sp,* splenial; *sq,* squamosal; *v,* vomer.

shape, with an anterior base and a posterior apex. The lateral temporal opening is, as noted above, elongate anteroposteriorly, in contrast to its much shorter span in most archosaurs; its posterior margin is somewhat convex in outline, suggestive of the initiation of the V-shape of this border in many archosaurs. In strong contrast with most archosaurs, the suspensorial region slants far back ventrally, the jaw articulation lying some distance back of the level of the occiput. The back margin of the suspensorial region is somewhat concave; this, plus a slight dorsal spur, shows the initiation of the type of otic notch characteristic of many more advanced archosaurs. The occiput slants diagonally downward and backward from the posterior margin of the narrow medial portion of the skull table.

Of individual dermal roofing elements, the premaxillae are elongate, in conformity with general snout elongation. They form most of the boundaries of the external nares. The premaxilla sends a long and well-developed process backward external to the naris, excluding the maxilla from the narial border and terminating in a slender tip between maxilla and nasal. Medially, conjoined slender processes from the two premaxillae form a narrow bar separating the nares and extending back some distance beyond the narial region to taper between and below the anterior tips of nasal processes that meet them. There is no evidence of a separate septomaxilla, reported as existing in this region in phytosaurs. Like the premaxillae, the nasals are elongate They enter into the posterior border of the external nares for a short distance and extend far backward to meet the frontals in a zig-zag transverse suture; laterally there is a long line of suture with the maxillae and a short contact with the prefrontals. The frontals, as indicated by the development of their radiating surface ridges, are somewhat elongated anteriorly. Laterally they have a long contact with the prefrontals anteriorly and a short posterior contact with the postorbitals; they enter broadly into the dorsal rims of the orbits. The parietals are short anteroposteriorly, as regards their development on the skull table. They have a transverse suture with the frontals in the middle portion of the roof; lateral to this, the line of suture with the frontals retreats sharply posteriorly, then turns forward again, allowing the parietals contact with the postorbitals. This lateral extension of the parietal forms the anterior border of the superior temporal

fenestra. The posterior end of the skull roof is narrow; on either side, however, each parietal sends, posterolaterally, a long process to meet and overlap the medial surface of the squamosal behind the superior temporal fenestra. Narrow dorsally but broadening below, the medial surface of this process forms the upper lateral boundary of the occipital plate and laterally forms the medial boundary of the superior temporal fenestra. This boundary is sharply marked off dorsally; more ventrally, however, the parietal slants outward to meet, obviously, the prootic area of the otic region of the braincase.

Laterally, the premaxilla continues back some distance along the margin of the upper jaw before being succeeded by the elongate maxilla. The latter element gradually increases in depth, posteriorly, to occupy the entire height of the side of the snout anterior to the antorbital fenestra. The maxilla extends upward beyond the ridge separating lateral and dorsal skull surfaces to form a lateral strip of the dorsal surface for, roughly, the length of the nasal. When the antorbital opening is reached, the maxilla extends but a short distance backward above this opening. Below, however, it forms the fenestral border for most of its length, to be finally succeeded by the jugal. Posteriorly the maxilla tapers downward in depth to terminate at about the level of the posterior border of the orbit. The lacrimal forms most of the bar separating orbit and antorbital fenestra and (although the line of suture is none too clear) appears to extend forward above this fenestra for most of its length on the lateral skull surface.

The prefrontal forms a triangular area on the skull roof, bounded medially by nasal and frontal, posterolaterally by the orbital margin and laterally by the ridge separating dorsal and lateral margins of the snout. It forms a prominent projection over the anterodorsal margin of the orbit and sends a process,

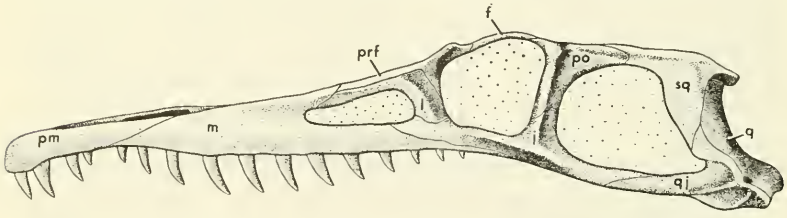

Figure 2. *Chanaresuchus bonapartei,* type skull in side view. × 4/9.

reinforcing the lacrimal, part way down the bar separating orbit and antorbital fenestra. There is no postfrontal element. The postorbital is well developed. Its center of ossification is a prominent elevation at the posterodorsal corner of the orbit, whence it extends in three directions. Medially, it extends over the skull roof surface to meet the frontal anteriorly and, more posteriorly, the parietal. This process forms anteriorly part of the orbital rim, and posteriorly a small portion of the boundary of the upper temporal fenestra. A posterior flange extends backward to form much of the upper border of the lateral temporal fenestra, gradually tapering backward to give place to the squamosal. Ventrally the postorbital extends downward to form the upper part of the bar separating orbit and lateral temporal fenestra. The jugal, in normal fashion, forms the lower margin of the orbit and much of the lower margin of the lateral temporal fenestra. Anteriorly it reaches the posteroventral margin of the antorbital fenestra, and it forms the lower part of the postorbital bar.

The squamosal, in a fashion somewhat analogous to the postorbital, sends out three processes from a center located dorsoposterior to the lateral temporal fenestra. An anteromedial process runs forward to join laterally the process of the parietal, which forms the medial wall of the superior temporal fenestra. A long and strong process runs anteriorly to meet the postorbital in a long diagonal suture and to form, in conjunction with that element, the bar lying between the lateral margin of the upper temporal fenestra and the upper boundary of the lateral temporal fenestra. A broad but thin process runs ventrally to form the posterior boundary of the lateral temporal fenestra; this meets the quadratojugal ventrally and posteriorly has a long suture with the quadrate. The squamosal, as in thecodonts generally, sends a short spur backward above the head of the quadrate. The quadratojugal forms the posterior part of the bar below the lateral temporal fenestra and then curves sharply upward to meet the squamosal and to form the lower part of the posterior margin of this fenestra. Posteriorly, at the junction of its two limbs, the quadratojugal is thickened and is in intimate contact with the quadrate.

As noted above, the occipital surface of the skull slants backward as well as downward. The posterior rami of the parietals form vertical walls that bound the occiput on either side. At the

apex of the occipital surface is a small triangular postparietal, which faces backward as much as upward and plays no part in the dorsal surface of the skull. Below this is a large supraoccipital, essentially triangular except for truncation of its narrow anterodorsal extremity. On either side this plate articulates with the proximal part of the posterior processes of the parietals. Dorsally the bone has a prominent medial ridge; ventrally this element forms the upper margin of the foramen magnum. The lateral margins of the foramen are formed by the exoccipitals, which are fused with the opisthotics to form long and slender paroccipital processes extending laterally to abut against the inner surfaces of the squamosals dorsally; this articulation is a loose one, with the presence of kineticism. Possibly a small posttemporal fenestra may have been present above the paroccipital process; if present, however, it cannot have been more than a slender slit. The exoccipital forms a dorsolateral fraction of the occipital condyle; the condyle is, however, mainly formed by the basioccipital. The condyle is circular in outline and essentially convex with, however, a slight median excavation, presumably for the anterior termination of the notochord. I regret that the condition of the material is such that I have been unable to make out the vagus and hypoglossal foramina nor the lateral surface of the braincase in the otic region. I have not found a stapes, and can say nothing regarding the possible presence of epipterygoid or laterosphenoid.

In correlation with snout elongation, the anterior part of the palate is much modified. Medially a pair of stout processes formed by the premaxillae extend backward in the midline; behind them, the central area is continued by narrow paired vomers, bearing a row of small teeth. Posteriorly the vomers diverge somewhat to accommodate between them the anterior tips of the pterygoids. At their posterior ends the vomers are in contact with the palatines, the anterior ends of which have a concave border, meeting the vomers medially and the elongate maxillae laterally.

In "typical" tetrapods the choanae are situated well forward, as rounded or oval openings, bounded anteriorly by the premaxillae, laterally by the maxillae, posteriorly by the palatines and medially by the vomers. If we look for the equivalent of the normal choanae here, we find a pair of long and narrow areas

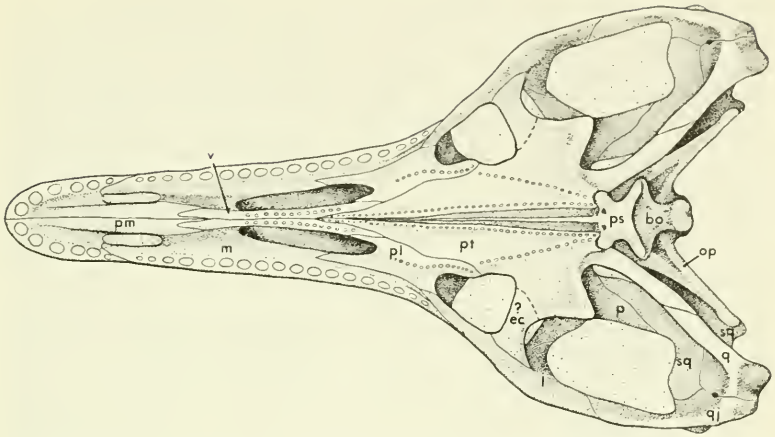

Figure 3. *Chanaresuchus bonapartei,* type skull in palatal view. × 4/9.

reaching about half the length of the skull, from the premaxillary region to the position of the "incised" anterior ends of the palatines. This elongation of the original choanal region is obviously related to snout elongation. From the palatines for some distance forward there are open choanae. But, farther forward, there is a sheet of bone apparently pertaining to the maxillae, which extends medially across the choanal areas from the maxillae to gain a contact with the posterior portions of the stout ventral processes of the premaxillae and the edges of the vomers. More anteriorly this sheet is broken by oval openings, already mentioned in connection with the skull roof. It is reasonable to believe that these openings are anterior palatine foramina for access to the mouth cavity of vomeronasal organs (Jacobson's organs), and that the transverse sheet of bone between these openings and the true choanae is a definite, if short, secondary palate formed for facilitation of underwater breathing in this long-snouted animal.

Much more normal and primitive in construction is the posterior portion of the palatal surface. Anterior to the occipital condyle, there are projecting basisphenoidal tubera, connected by an incised transverse line, concave posteriorly, which presumably marked the anterior limit of subvertebral musculature.

Lines extending posteromedially from the tubera suggest an extension of parasphenoidal dermal ossification backward over part of the basioccipital area. Anterior to the tubera, the combined basisphenoid-parasphenoid contracts somewhat in width, then expands again to the projecting spherical basal articular processes, on which it is obvious the pterygoids had considerable freedom of movement. Paired foramina for the carotid arteries are present between these processes. A slender parasphenoid rostrum extends far forward along the midline of the interpterygoid vacuity. Of the elements of the posterior part of the palate, the palatine occupies an area between the posterior end of the choana anteriorly and the palatine fenestra posteriorly, and between the maxilla laterally and the pterygoid medially. It bears ventrally an anteroposterior row of small teeth. The pterygoids are highly developed. Their slim anterior ends extend far forward between the vomers. A short distance back of their anterior termination the two pterygoids diverge slightly, so that a long but narrow interpterygoid vacuity is developed. Along the medial border each pterygoid carries a long row of small teeth; this series terminates just above the region of the basal articulation with the braincase. A second row of small teeth is present on a distinct ridge that slants diagonally backward and medially from a point near the posterior end of the palatine to terminate somewhat short of the basal articular region. The palatal fenestra is of considerable extent, bounded laterally by the jugal and incised medially into the posterior part of the palatine and the adjacent portion of the pterygoid. Back of the fenestra the palatal ramus of the pterygoid expands widely laterally. Part of this expansion is presumably formed by an ectopterygoid, but I have not been able to detect a pterygoid-ectopterygoid suture. Anteriorly the lateral margin of this expansion is sutured to the jugal; posteriorly there is a constriction in width, and the bone slants ventrally to form a stout transverse pterygoid flange, broadening distally. The palatal portion of the pterygoid terminates medially and posteriorly in a short spur beneath which is the socket for reception of the articular process of the basisphenoid. Lateral to this area, there arises a typical quadrate flange of the pterygoid, of modest height, which posteriorly meets the quadrate.

The quadrate bone is well developed. Its posterior end is a thickened articular area, widened transversely and convex at both internal and external ends; it appears that the quadratojugal (as often) takes part to some degree in the lateral condyle. The main shaft of the quadrate extends upward, to terminate in a recess on the under surface of the squamosal at and close to its posterior spur. This ascending ramus of the quadrate is broad ventrally, gradually contracting in width dorsally, and has a concave posterior margin. It faces as much posteriorly as laterally, at an angle to the adjacent areas of the quadratojugal and descending ramus of the squamosal. As generally, a foramen is present on this surface between quadrate and quadratojugal. The ascending ramus presents a broad, forward-slanting, medial surface that is covered anteriorly by the quadrate ramus of the pterygoid.

In correlation with skull length, the jaw is long and slender anteriorly (Figs. 4, 5). The symphysis is poorly represented in available material but was obviously weak and formed mainly — perhaps entirely — by the dentary. For much of the length of the muzzle the dentary forms almost the entire outer surface of the ramus — a surface that slants markedly inward below, rather than being directed vertically downward. Posteriorly the bone forks, the two branches enclosing between them the anterior end of the long external mandibular fenestra. The upper branch extends along the upper margin of the ramus to the end of the tooth

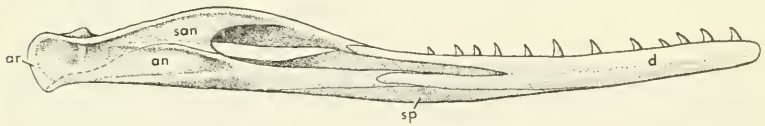

Figure 4. *Chanaresuchus bonapartei*, jaw of type in lateroventral view. × 4/9.

row, where it is replaced by the surangular; the lower branch extends backward below the fenestra for some distance, applied to the outer surface of the angular. The splenial is exposed at the lower edge of the external surface. The posterior portion of the external surface is made up almost entirely by the surangular and angular. The former bone runs backward along the curving

upper margin of the ramus, whence a dorsally facing area of the surangular extends inward above the lateral border of the mandibular fossa. The angular extends backward below the lateral mandibular fenestra, the two elements meeting at the posterior end of the fenestra, whence a ridge, with which the suture between the two elements is associated, runs posteriorly. The suture is indistinct posteriorly but the conjoined angular and surangular extend backward nearly to the posterior end of the jaw, sheathing the articular laterally. On the inner surface the splenial lines the jaw for nearly its full height for most of the length of the tooth row. Beyond this point its upper margin slants gradually downward to the termination of the bone well posteriorly. It is succeeded posteriorly on the inner surface by the prearticular, which, narrow anteriorly, follows the splenial downward and backward. The prearticular forms the inner border of the mandibular fossa, the surangular the outer border. A coronoid is present, but seen only as a disarticulated element. I have restored it, in Figure 5, with some doubt, in its probable position. It appears to have extended forward as a thin sliver

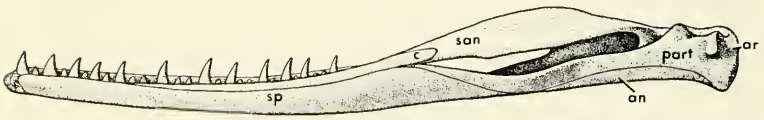

Figure 5. *Chanaresuchus bonapartei,* jaw of type in medial view. × 4/9.

of bone between the dentary and splenial and more posteriorly appears to have been applied to the inner surface of the surangular. Posteriorly, the surangular thickens on its inner surface to form the back margin of the mandibular fossa. The prearticular fuses posteriorly with the articular. This stout element appears to have been but loosely attached to the surangular and angular, since it has separated from them in the two available specimens with jaws in the La Plata-Harvard collection. The articular occupies the full height of the inner surface of the jaw at its posterior end; it is braced anteriorly by the medial extension of the surangular mentioned above, and is nearly completely covered externally by the thin posterior extension of the conjoined angular

plus surangular. There is little development of a retroarticular process, but the bone extends somewhat ventroposteriorly. The articular surface of the articular, as of the quadrate, is transversely broadened, with median and lateral concavities corresponding to the pair of convexities on the quadrate. There is a pronounced process developed on the medial surface just below the level of the articular surface.

The marginal dentition is but imperfectly preserved in available specimens. The teeth are of a common archosaurian type, somewhat compressed mediolaterally, hence with an oval section, sharp-pointed, and backwardly curved distally. The insertion is protothecodont. There appear to have been six teeth, the last small, on the elongate premaxilla, about 18 on the maxilla, and about the same number on the dentary. As in many reptiles, there appears to have been a high degree of replacement of teeth in essentially alternating fashion, so that for much of the jaw length alternate teeth are well developed, those between barely erupted or represented by empty sockets.

Gualosuchus reigi, gen. et sp. nov.

Holotype. La Plata Museum 1964–XI–14–13 (field no. 75), including most of the right half of skull and jaws and a limited amount of postcranial material. Collected from the Chañares Formation, from the valley of the north fork of the Chañares River, La Rioja Province, about five miles east of the point where this stream debouches into the Talampaya plain.

Combined generic and specific characters. Similar to *Chanaresuchus* in nearly all regards, but larger; posterior portion of skull deeper but with a narrower skull table than in *Chanaresuchus;* orbit taller than in that genus and less incised into skull roof; parietals extend in paired fashion farther back on skull table than in *Chanaresuchus* and diverge less sharply posteriorly toward the squamosals; superior temporal openings proportionately narrow and more elongate.

The generic name, by analogy with *Chanaresuchus,* refers to the Gualo River, which, with the Chañares, drains most of the known area of exposure of the Chañares Formation. The specific name is in honor of Sr. Osvaldo A. Reig, an active student of archosaur evolution.

Gualosuchus is represented in the Harvard-La Plata collections only by the holotype, which includes the dermal bones of the right side of the skull roof, the pterygoids, right palatine, most of the right lower jaw and a number of postcranial elements. Further materials, including a second skull, are present in the Instituto Lillo collections. The length of the holotype skull (Figs. 6, 7), measured to the quadrate, is about 325 mm; the Instituto Lillo skull, presumably that of a young individual, is much smaller. Quite probably the holotype represents a "mature" specimen; it is nearly a quarter larger than the largest known skull of *Chanaresuchus*. The skull of the holotype is highly rugose, presumably in correlation with large size; this feature has made identification of sutures difficult.

In every major structural feature the *Gualosuchus* skull closely resembles that of *Chanaresuchus*. In consequence, detailed description is unnecessary; mention need be made only of points in which the two genera differ. As in *Chanaresuchus,* the skull is long and low; the proportions of snout length to total skull length are much the same in the two genera, and both have the same anteroposterior elongation of the lateral temporal fenestra. The skull of *Gualosuchus,* however, is much less depressed posteriorly than that of *Chanaresuchus,* and less broad. In *Chanaresuchus,* for example, the height of the skull at the orbit is little more than 15 per cent the skull length; in *Gualosuchus* about 22 per cent, and the comparable figures at midlength of the lateral temporal fenestra are 17 per cent and 24 per cent. In relation to greater depth at the orbit, this opening, which is subcircular in lateral view in *Chanaresuchus,* is taller and subquadrate in shape in *Gualosuchus* and is much less incised into the skull roof. Part of the contrast in depth is due to the greater depth of the maxilla and jugal beneath the antorbital vacuity, orbit, and the anterior part of the lateral fenestra. The differences in breadth between the two genera relate mainly to differences in width of the skull table. In *Chanaresuchus* the width across the postorbital-squamosal bars bordering the skull table on either side, is nearly a third the measurement of skull length; in the *Gualosuchus* type this width is but a quarter the skull length. This difference in table proportions results in contrasts in the pattern of the posterior part of the skull roof. In *Chanaresuchus* the superior temporal fenestrae are relatively short and broad

and slant outward posteriorly; in *Gualosuchus* these openings are relatively long and narrow and lie on a directly anteroposterior line. In *Chanaresuchus* the two parietals are united on the skull table for only a short distance before they diverge sharply to extend outward and backward to meet the squamosals; in *Gualosuchus,* in contrast, the parietals extend backward in contact with one another for a considerable distance before diverging, at a lesser angle, toward the squamosals.

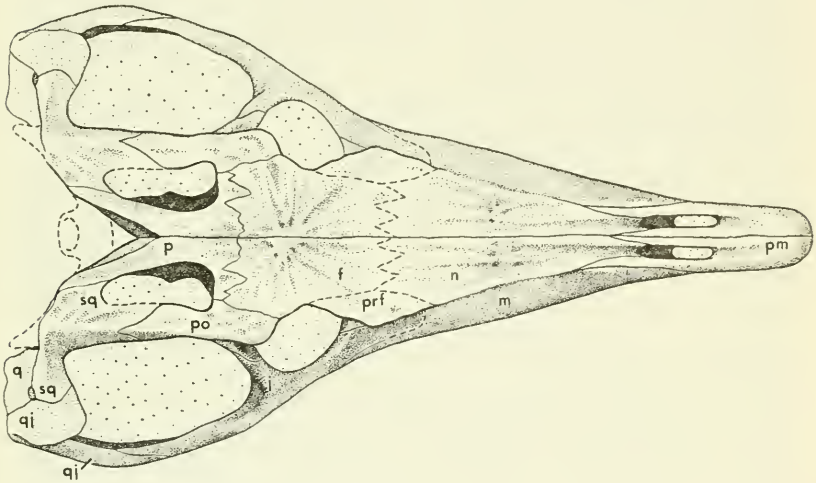

Figure 6. *Gualosuchus reigi,* holotype skull in dorsal view. × 1/3.

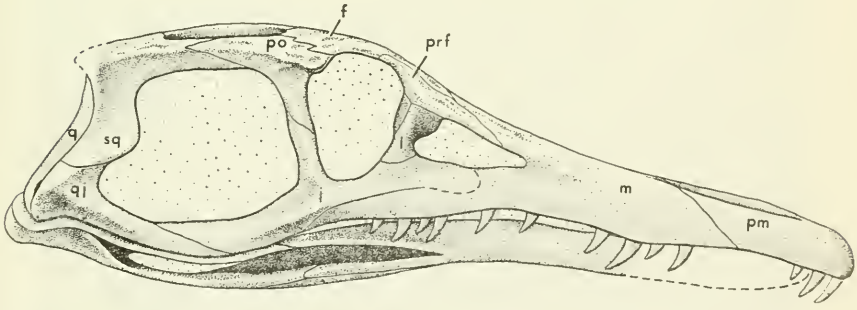

Figure 7. *Gualosuchus reigi,* holotype skull in lateral view. ×1/3.

The disarticulated pterygoids and right palatine are very similar in construction to those of *Chanaresuchus*. Most of the right ramus of the lower jaw is preserved in the type. It had been somewhat weathered before recovery, but in all observable features it agrees well with the *Chanaresuchus* jaw.

DISCUSSION

Chanaresuchus and *Gualosuchus* are closely related; they appear to be almost identical in all structural features and as far as known differ only in size and in skull proportions, the *Gualosuchus* skull being relatively narrower and taller posteriorly. We need not search far to find relatives. It is obvious that *Cerritosaurus* described by Price (1946) from the slightly later Santa Maria beds of Brazil is a close relative, as shown by similar skull proportions, slitlike dorsally-placed nostrils, loss of postfrontal element, absence of the parietal foramen, comparable shape of the lateral temporal fenestra, and posterior situation of the jaw articulation. Possibly some of the thecodont material from the Manda beds may pertain to a related type, but this material is too fragmentary to allow positive determination.

Quite surely, however, a further South American relative is *Proterochampsa* (Reig, 1959; Sill, 1967). A number of points of resemblance to *Chanaresuchus* and *Gualosuchus* can be seen in the figures of Reig and Sill, and further unpublished observations and study of the *Proterochampsa* specimens in the light of our better knowledge of the Chañares forms strongly suggest that the relationship is close indeed. The *Proterochampsa* skulls are even more flattened than in *Chanaresuchus* (although this may be due in part to post-mortem crushing). The skull is sculptured as regards its dermal roofing elements in very rugose fashion, presumably in correlation with the fact that its size is considerably greater than that of either of the Chañares forms. This rugose condition makes for difficulty and doubt in the determination of sutures. The skull proportions, with a long slender snout and a broad posterior region, are identical with those in the earlier genera. The outlines of the external nares are imperfectly preserved, but the structure here is apparently the same as in *Chanaresuchus* and *Gualosuchus*. The antorbital fenestrae are small, as in those genera; the orbit, subcircular in shape as in *Chanaresuchus,* is strongly incised into the skull table; because

of the great flattening of the skull, these openings face nearly directly dorsally rather than laterally. The pattern of the posterior part of the skull table, with a pineal opening absent, and the posterolateral extensions of the parietals swinging broadly outward, closely resembles that of the Chañares genera. As in those forms, the lateral temporal fenestra is large and long anteroposteriorly; the jaw articulation is far back of the occiput, and, as in the earlier genera, there is but a slight projection of the squamosal above the incipient archosaur otic notch. The lower jaw structure, as far as can be made out, is similar to that of the forms here described.

The palate is poorly seen, but recent study indicates that the posterior portion of it was quite similar to that of *Chanaresuchus* and *Gualosuchus*. As in those genera, the basal articulation was movable and an interpterygoid vacuity present, in which, as in the genera here described, there projected forward a slender parasphenoidal rostrum. A row of denticles was present, as in the Chañares forms, on the palatine as well as denticle rows on the pterygoid.

Again, as in these forms, the anterior ends of the palatines were notched for the posterior margins of the choanae. Forward of this point little can be made out regarding palatal structure. Both Reig and Sill restore this area with a small choana and a long secondary palate. This is, however, uncertain and the situation here may well have been much the same as in the Chañares forms.

In sum, *Proterochampsa* in all observable features appears to be very similar in cranial structure to *Chanaresuchus, Gualosuchus* and *Cerritosaurus;* the differences between them are certainly not more than of generic value, and all four may be reasonably grouped within the single family Proterochampsidae, erected by Sill (1967) for the reception of *Proterochampsa.*

The general structure of these four genera is strongly suggestive of amphibious habits, not improbably paralleling those of the later phytosaurs and crocodilians. The postcranial skeleton appears to have the general proportions of crocodilians (although without diagnostic crocodilian characteristics). The slender snout, flattened skull, the trend for a dorsal facing of the orbits and the dorsal position of the nostrils are all suggestive of water-dwelling habits.

What is the pedigree of these forms? Currently, as regards classification of thecodonts, one tends to sort out a few early and primitive genera as the Proterosuchia, separate off as advanced types the Phytosauria and (in some fashion or other) crocodilian ancestors, and, having done this, "lump" all remaining forms as members of the suborder Pseudosuchia. One's first inclination would be to include the Proterochampsidae in this last general category. Further consideration, however, suggests that the proterochampsids are too primitive structurally to be placed in the Pseudosuchia. In a few regards our forms are advanced or specialized — dorsal position of the nares, loss of the postfrontal and of the parietal foramen, structure of the anterior part of the palate, and an advanced jaw structure. But there are many primitive features — for example, small size of the antorbital opening, posterior position of the suspensorium, long anteroposterior extent of the lateral temporal fenestra, presence of a movable basal articulation, retention of an interpterygoid vacuity and retention of palatal teeth. Typical pseudosuchians are advanced in all these characters. *Euparkeria,* recently well described by Ewer (1965), which is either reckoned as a primitive pseudosuchian or as an advanced proterosuchian leading toward the pseudosuchians, is as primitive as the proterochampsids in most of the features listed. But even *Euparkeria* is more advanced in some features, such as the relatively large antorbital fenestra and, more significantly, shortening of the lateral temporal fenestra and forward movement of the suspensorial region.

One is thus tempted to consider a direct origin of the proterochampsids from a proterosuchian ancestor. Charig and Reig (1970) list some 27 structural features that are characteristic of proterosuchians, 16 of which (2–17) pertain to the cranium. In the greater part of these characters, the Proterochampsidae are in agreement with the Proterosuchia. They differ in a few points: (2, part) absence of a postfrontal and of a parietal foramen; (5, part) nonterminal position of external nares; (9) a slight projection of the squamosal back beyond the head of the quadrate (present, however, in *Chasmatosaurus*); (13) formation of an incipient secondary palate; (14) the presence or absence of an epipterygoid is unknown. In all other points the Proterochampsidae are in full agreement with the Proterosuchia: (2, part) a median postparietal present; (3) well-developed and projecting

prefrontal; (4) short and broad parietal; (5, part) exclusion of maxilla from naris by premaxilla; (6) moderate size of antorbital vacuity; (7) superior temporal fenestra facing dorsally; (8) no V-shaped lateral temporal fenestra; (10) little development of otic notch; (11) jaw articulation well behind condyle; (12) interpterygoid vacuity present; (15) marginal teeth more or less isodont; and, (16) tooth insertion subthecodont. To this long list of primitive characters may be added the presence of a movable basipterygoid articulation, and retention of palatal teeth. It seems clear that the Proterochampsidae are of direct proterosuchian derivation and, despite a few advances, may best be classified as a family of the Proterosuchia.

Further, one's attention can be immediately directed to *Proterosuchus* [*Champsosaurus*] as a proterosuchian probably not far removed from the near ancestry of the Proterochampsidae. Reig (1959), Sill (1967), and Walker (1968) have each in turn commented on the similarity of *Proterochampsa* to "*Chasmatosaurus*." Apart from the nasal apparatus, little change is needed to transform *"Chasmatosaurus"* into a proterochampsid — reduction of the downward curvature of the snout, loss of the postfrontal bone, and modification of the posterior part of the lower jaw. Two changes anteriorly are needed — an upward and backward shift of the external nares and, with further elongation of the already slitlike choanae of "*Chasmatosaurus,*" initiation of a secondary palate. The proterochampsids can be reasonably considered to be direct and relatively unmodified descendants of a proterosuchian of "chasmatosaurid" type.

Were the Proterochampsidae a sterile line or could they have given rise to more advanced archosaurs of any sort? The two possibilities are the Phytosauria and Crocodilia. Reig and Sill believe *Proterochampsa* to be an ancestral crocodile; Walker (1968, 1970) denies the crocodilian affinities of *Proterochampsa* but suggests relationships to phytosaurs, while, on the other hand, he suggests that *Cerritosaurus* is a crocodile relative.

I see little positive evidence to support relationship of any member of the Proterochampsidae to the Crocodilia. As far as I am aware, the postcranial skeleton of *Chanaresuchus* shows none of the significantly crocodilian features of coracoid, pubis, etc., that are characteristic of Triassic "pre-crocodilians." As regards the skull, Reig calls attention, in addition to the beginning of a

secondary palate, to the rather crocodilian skull proportions, particularly those of the table. Sill gives a careful and detailed analysis of skull structure, but, apart from the secondary palate, cannot point out any feature in which *Proterochampsa* approaches crocodilian conditions; at best, it exhibits features that may have been present in the remote ancestors of the Crocodilia, and that are, essentially, those present in generalized ancestral thecodonts. The posterior portion of the palate, for example, is of an extremely primitive pattern, markedly modified in all nonproterosuchian thecodonts. Notably primitive is the suspensorial region, with the jaw articulation far to the rear of the occiput and the lateral temporal opening greatly elongated. To attain the crocodilian condition it seems structurally necessary for this region to pass through the pseudosuchian stage of a short lateral temporal region with a V-shaped posterior boundary, followed by closure of the upper part of the lateral vacuity, a forward shift of the upper end of the quadrate and, finally, downward closure of the squamosal back of the otic notch. There is not, in proterochampsids, the slightest trace of the beginning of this highly important series of structural changes; these forms are not a whit more advanced than the archaic thecodont "*Chasmatosaurus*." The posterior part of the proterochampsid jaw, again, is specialized in a noncrocodilian fashion. Finally, the movement of the external nares upward and backward along the skull roof is a structural feature that is not primitive or merely "neutral" in nature, but is in direct contrast to the situation expected in an ancestor of the Crocodilia, in which the nostrils are persistently terminal in position in almost every case.

In short, for positive signs of crocodilian relationships of the proterochampsids, we are reduced to the presence of a short secondary palate. It is possible, but difficult, to imagine this structure being expanded and modified to form the elongate secondary palatal structure seen in true crocodilians. It seems more probable, at present, to believe that the development of this structure plus the backward movement of the external nares, represent an attempt, parallel to that of crocodilian ancestors, to improve respiration in a long-snouted amphibious reptile.

If we turn from the proterochampsids to a series of later Triassic archosaurs, such as *Notochampsa, Erythrochampsa, Protosuchus,* and the recently described *Orthosuchus* (Nash,

1968; cf. Walker, 1970), we find a series of forms in which there is little development of a secondary palate, but in which there are numerous positive indications of crocodilian relationship, such as the series of crocodilian postcranial characters that are absent in proterochampsids, progress in the development of the crocodilian type of suspensorial and otic regions, presence of supraorbital bones, fusion of braincase and palate ventrally. There is little indication that these forms are directly derived from such archaic and essentially proterosuchian forms as the proterochampsids; rather, it would seem, the crocodile ancestors advanced from the proterosuchian to the pseudosuchian stage of thecodont development, and then began to specialize in the direction of the Crocodilia.

Although Walker (1968), as noted above, suggested that *Cerritosaurus* might be related to crocodilian ancestry, he denies this for its relative *Proterochampsa,* and suggests, in contrast, that this genus might have been ancestral to the phytosaurs. Most of the items listed by him as phytosaurian similarities appear to be of little weight and could be countered by other features wherein *Proterochampsa* differs from possible "proto-parasuchians" (as, for example, in loss of postfrontals in proterochampsids). The one seemingly important and suggestive feature is the movement of the nares, as slitlike structures, well back onto the dorsal skull surface. This could well be an initiation of the strong posterior narial trend seen in phytosaurs. But in default of intermediate forms, the gap between such a proterochampsid as *Chanaresuchus* and a typical phytosaur is so great as to make an assumption of relationship, in the present state of our knowledge of thecodonts, little more than an interesting possibility.

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